Competition for nitrogen

and

moisture in a

Pinus radiata - pasture agroforestry system

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Abstract

A 3 x 2 factorial experiment was conducted to examine the outcome and some of the competitive mechanisms between *P. radiata* (D. Don) and pasture for N and soil moisture. The factors examined were the monthly addition of 30 kg N/ha versus no additional N, and the manipulation of the level of pasture competition by spraying and simulated-grazing to give three levels of pasture competition. The experiment coincided with a period of severe drought which greatly increased the competition for soil moisture.

Removal of pasture competition by spraying released a large amount of N into the soil mineral N pool. It also reduced overall demand for N and water because of the reduction in competition resulting in improved tree growth and greater N uptake by trees. However, it was apparent that moisture was the main limiting factor for tree growth in the plus-pasture treatments because, whilst trees did take up some of the applied N in the plus-pasture treatments, they showed no increase in growth and N uptake.

A localized effect of trees on pasture dry matter production and N content occurred. Directly beneath trees and in the area predominantly occupied by tree roots competition for water and N was intense. Pasture response to N was greatest away from the tree rooting zone. Pasture appeared to compete successfully due to the nature of its root system which consists of a large biomass of very fine roots compared to the small biomass of fine pine roots in the surface soil.

Competition between pasture and trees was further examined using the stable isotope ^{15}N to trace a single ^{15}N-labelled application of N fertilizer in spring. Recovery of ^{15}N during the split fertilizer application program was assessed by periodic pasture harvests in the simulated-grazing treatment and by obtaining a complete balance sheet after 249 days.

The dynamics of plant availability of applied ^{15}N and retention of ^{15}N in the soil was also followed. The recovery and retention of $^{15}NO_3^-$ and $^{15}NH_4^+$ in particular were compared in the simulated-grazing treatment. Larger quantities of $^{15}NO_3^-$ remained available to plants than $^{15}NH_4^+$ and ^{15}N was still found in the KCl-extractable mineral N pool at 154 and 249 days after application. *P. radiata* assimilated the same amount of ^{15}N when added as $^{15}NO_3^-$ or $^{15}NH_4^+$ in the simulated-grazing treatment but uptake into the aboveground biomass of pasture was greater for $^{15}NO_3^-$ than for $^{15}NH_4^+$. However, pasture uptake of $^{15}NO_3^-$ and $^{15}NH_4^+$ was not significantly different when pasture stubble and roots were include in the total recovery for all harvests. Removal of pasture competition increased the availability of ^{15}N for the period just after application but ^{15}N uptake by *P. radiata* was only doubled.

There were no significant differences in ^{15}N recovery between treatments in the 0-20 cm depth of soil; on average this was 49% of that applied. Total system recovery was 107, 92, 76, and 71% for the $^{15}NO_3^-$-treated, $^{15}NH_4^+$-treated simulated-grazing treatments, $^{15}NH_4^+$-treated rank, and sprayed treatments, respectively. The loss of ^{15}N from the system was not accounted for by leaching although this was not directly measured. In the sprayed treatment where the loss of ^{15}N was greatest, it was thought that ^{15}N loss may have been due to denitrification.

The root systems of neighbouring trees did not overlap and midway between the trees there was apparently no competition between trees and pasture since no effect of tree roots on pasture growth and ^{15}N uptake could be shown.

Uptake by artificially-grazed pasture did not seem to reduce ^{15}N movement into the canopy to the same extent as uptake by rank pasture. In the simulated-grazing treatment the increased cycling of N or reduced pasture root growth may have provided some benefit to tree uptake of ^{15}N.

Chapter One

Introduction

1.1 Introduction

The forestry sector in New Zealand is undergoing a period of great change in terms of its administration and ownership and the future direction of management. This period of change was heralded by the reorganization of the New Zealand Forest Service into a Ministry of Forestry, Forestry Corporation and a Department of Conservation. The agricultural sector has also been restructured, a process that has been driven by the removal of subsidies. These changes in institutional arrangements have also created considerable interest in the relationship between agriculture and forestry (O'Conner, 1986), with traditional concepts of single purpose land management being reconsidered.

In the past, the relationship between agriculture and forestry has been a practice characterized by *distinct* and *separate* land use options both on a regional and on a farm level. Reasons for this have been discussed elsewhere (O'Conner, 1986). Currently, agroforestry, a term relating to *dual* land use options, is being considered as an important initiative in the design and practice of sustainable land use policy. It is frequently argued that this land use option is more profitable than single purpose options (Anderson *et al.*, 1988) and brings diversification to the farm income. However, agroforestry requires greater management skills and a better understanding of the ecosystem.

The usual definition of agroforestry is "the deliberate growing of woody perennials on the same unit of land as agricultural crops and/or animals, either in some form of spatial mixture or in a sequence" (The Editors, 1982). This can be expanded to include "there must be a significant interaction between components of the system, either ecologically and or economically". In this particular study we use the definition of Lewis and Pearson (1987) which refers to the deliberate mixing of pines and pasture for grazing.

The work described in this thesis focuses on the outcome of competition between *Pinus radiata* D. Don and pasture for N and some of the mechanisms involved at the ecosystem level, with the emphasis on nutrient cycling and moisture. Thus, as part of a monthly fertilizer application program, ^{15}N-labelled fertilizer was applied on one occasion to *P. radiata* growing with three levels of competition from pasture. The ^{15}N-labelled fertilizer was used as a tracer to examine the competition for N between the trees and pasture. In addition, soil moisture was investigated as it is thought to play an important role in competition.

Agroforestry studies to date, in general, have lacked an examination of the nutritional/moisture relationships in the ecosystem. These need to be understood in more detail to enhance and optimize the management system. It has been assumed that the improved growth of radiata pine is due to the high N status of these sites coupled with an increased rate of nutrient cycling caused by the grazing animal, without actually investigating the ecosystem processes. Steele and Percival (1984) have suggested that radiata pine competes strongly with pasture for N. Other establishment studies show that radiata pine is typically susceptible to competition for water from other vegetation and in some cases N is implicated as well. The importance of studying the movement of ^{15}N in the whole ecosystem is seen from the example of Steele and Percival's study, as there was little evidence presented to support their claim that radiata can take up large quantities of applied N.

The purpose of this study was to quantify the N dynamics in a pine-pasture ecosystem, and to determine how N and moisture were involved in the competition between the two. The experimental work undertaken to meet this purpose had the following specific objectives:

1. to quantify the effect of pasture competition on the growth, and N uptake by *P. radiata* at two levels of N supply;

2. to assess the uptake of ^{15}N by pasture and *P. radiata* and its recovery in the soil, at different levels of competition between trees and pasture to determine the extent of competition for N and the likely benefits of grazing to tree growth;

3. to examine the form of N preferred by the pasture and the trees in a simulated-grazing situation;

4. to examine the effect of pine roots on pasture growth and N uptake;

5. to monitor soil N processes and moisture changes to assist interpretation of the competitive effects.

1.2 Contrasts in nutrient cycling between forestry and pastoralism

Conventional forestry and pastoral ecosystems differ in their fundamental processes of nutrient cycling and management systems. This has consequences for our understanding of nutrient cycling in agroforestry ecosystems. Forest ecosystems typically have a large N capital but very small quantities are in plant-available forms, less than one percent of the total (Carlyle, 1986). Therefore, the growth of forests depends upon biogeochemical and biochemical cycling of N in their ecosystem.

In acid forest soils the dominant form of N available to trees is NH_4^+ (Keeney, 1980). Nitrate is considered to be unimportant in undisturbed forests (Vitousek *et al.*, 1982). However, many forest plants (Smirnoff *et al.*, 1984), including *P. radiata* (McFee and Stone, 1968; Adams and Attiwell, 1982a and b), can utilize both NH_4^+ and NO_3^-. Much of the N uptake by vegetation in forests originates from the decomposition and release of nutrients from organic matter. In contrast, N cycling in pastoral agriculture is typified by the return of nutrients to soil via dung and urine. Only a small percentage of the annually produced plant N is removed by the grazing animal. The effects of animals on the mechanisms of N cycling in pastoral systems have been reviewed by Floate (1981). Grazing speeds up the N cycle (Quinn, 1982) but also increases potential loss of N through increased volatilization and leaching from dung and urine patches.

Furthermore, the temporal and spatial distribution of N from dung and urine may limit the benefits to be gained (Scott, 1973). In spring or early summer low soil temperatures may limit N mineralization and also clover growth. This results in low concentrations of N and hence pasture becomes N stressed. Stock behaviour also results in the uneven distribution of dung and urine partly due to stock camps (During, 1984).

Intense competition between the trees and pasture appears to be symptomatic of an agroforestry system. Competition for light, water and nutrients might be anticipated. Forest managers are aware of the consequences of competition between trees and weed species in that weed control is considered important in early forest establishment to ensure good tree survival and rapid early growth (Balneaves, 1982).

P. radiata in agroforestry situations shows increased basal area growth (Knowles and Percival, 1983), which is thought to be related to the lower stockings and higher nutrient status of agricultural situations, although this has not been proven. Furthermore, the role of the grazing animal has not been elucidated.

1.3 Soil moisture and *P. radiata* growth

Rook *et al.* (1976) discussed the reaction of *P. radiata* to drought; stem diameter and root growth were initially affected by the onset of drought. Following these effects, rates of transpiration and then photosynthesis were next reduced. At extreme moisture stress, older foliage was shed. A detectable response to re-watering in rates of transpiration and photosynthesis occurred within two days. Similarly, a rapid response to watering was observed by Benecke (1980). Jackson *et al.* (1976) observed that basal area increment was restricted by current soil moisture deficit during the months of December through April. However, the reduction of drought stress in trees by the extraction of water from deep within the soil profile has been observed by Jackson *et al.* (1983).

The growth of *P. radiata* under optimum soil water conditions has rarely been examined because the usual condition of summer drought and its effects on the growth of *P. radiata* have preoccupied researchers. Cromer *et al.* (1983) demonstrated the increase in the growth of *P. radiata* when the species was irrigated with waste sewage water. However, even the growth of irrigated 10-year-old *P. radiata* was reduced during severe drought (Linder *et al.*, 1987).

The biggest increase in tree growth occurs when irrigation is combined with fertilizer. This improved growth of *P. radiata* due to both irrigation and fertilization may be attributable to either an increased rate of photosynthesis per unit leaf area (Linder and Rook, 1984; Field and Mooney, 1986) or a change in allocation of photosynthate from roots to shoots (Bevege, 1984).

1.4 Indirect effects of trees on pasture

Pasture production under *P. radiata* relative to open pasture has been shown to decline with increased stocking of *P. radiata* and/or increasing total crown length/ha (Percival and Knowles, 1988). However, in young stands at low stocking, pasture production may be higher than in open pasture (Cossens, 1984). The exact nature of this interaction was not quantified. Russell and Grace (1979) described the effects of increasing windspeed on grass growth as a decline in mean relative growth rate of the whole plant. Water stress was implicated as an important cause of reduced growth due to wind. It is possible that young wide-spaced stands have a sheltering effect on pasture growth. The effect of shelterbelts on pasture production has been quantified by Radcliffe (1985). Increased pasture production was associated with a decreased windrun and higher soil moisture in sheltered areas. Anderson and Batini (1979) observed that soil moisture content down to 30 cm was higher under 12-13-year-old *P. radiata* than in open pasture and this was attributable to improved water retention in the soils under trees due to a sheltering effect.

1.5 Nitrogen and the growth of *P. radiata*

Many experiments show that the addition of large amounts of N to soil increases the growth of *P. radiata* (Knight, 1973; Will, 1977; Mead and Gadgil, 1978). The seminal paper of McFee and Stone (1968) demonstrates the NH_4^+ preference of *P. radiata*. However, the consequences of the observation that *P. radiata* also grows well with NO_3^-, as compared with the control, has been overlooked by at least Knight (1973) and Will (1977). These authors did not consider the possible occurrence, and importance, of N transformations in soils when interpreting the results of their experiments, probably because they were more concerned with normal acid forest soils. Adams and Attiwell (1982a and b) have demonstrated nitrate reductase activity in *P. radiata* roots. These observations have important implications for the current understanding of *P. radiata* nutrition and N cycling in agroforestry. Work by M.F. Skinner (pers. comm.) indicates that non-mycorrhizal seedlings of *P. radiata* preferred NO_3^- to NH_4^+. The preference of mycorrhizal seedlings is not established convincingly by Skinner and nor has the preference, if any, of *P. radiata* for NO_3^- or NH_4^+ been established conclusively. This is further confounded by conflicting evidence about N preferences of other conifers (Van den Driessche, 1971; Van den Driessche and Dangerfield, 1975; Preston *et al.*, 1990).

Recovery of ^{15}N-labelled NO_3^- fertilizers for several conifer species is higher than ^{15}N-labelled NH_4^+ fertilizers (Nommik, 1966; Melin *et al.*, 1983; Melin and Nommik, 1988; Nommik and Larsson, 1989). Although in some cases these differences are not significant, the trends suggest that trees prefer to take up NO_3^-. In some cases the high recoveries of ^{15}N-labelled NO_3^- fertilizers may be confounded by differing soil reactions: NH_4^+ is immobilized more rapidly than

NO_3^- therefore plants are more easily able to use NO_3^- in the short term. The N preference of *P. radiata* has not been examined with ^{15}N techniques and, despite the limitations of these techniques, information on N preference would add to our understanding of the growth of *P. radiata*.

1.6 Pasture response to nitrogen

Pasture responses to applied N are common (During, 1984; Steele and Percival, 1984). Although white clover may fix large quantities of N, this N fixation is poorly distributed in both time and space. Therefore, in early spring when soil temperature is low and mineralization of mineral N is reduced, responses to added fertilizer N are possible due to the high growth potential of pasture species.

Ledgard *et al.* (1989) examined the effect of simulated winter temperatures on pasture growth and found that the pasture response to added N was greater in a cold winter than in a mild winter. More N was immobilized in the cold winter.

1.7 Competition for nitrogen and water

An individual plant competes in the soil for limited resources that may be as limiting to its competitors (other plants and soil microbes) as they are to the plant itself. Therefore, with N fertilizers it is important to examine how these competitors, as well as the desired plant, respond to additional N. For example, competition for N between processes of the N cycle (e.g. immobilization) and grass vegetation reduced the growth of *Eucalyptus delegatensis* seedlings on an N-deficient site (Ellis *et al.*, 1985). It was found that manual weeding increased N concentrations in seedling tissues and improved seedling growth and also resulted in higher levels of soil mineral N.

Tree-pastures competition trials are important in the study of agroforestry. For example Hedrick and Keniston (1966) found sheep grazing improved soil moisture content and trees on grazed plots grew better. Grazing reduced competition from palatable species. Similarly, Doescher *et al.* (1989) report enhanced water relations and growth of conifer seedlings due to controlled cattle grazing. However, grazing is not as effective as conventional weed control with herbicides. Weed control not only reduces water stress temporarily but may also influence nutrient cycling.

The effect of weed control on the establishment and early growth of *P. radiata* has been widely studied (Squire, 1977; Cellier and Stephens, 1980; Nambier and Zed, 1980; Sands and Nambier, 1984). For example, Squire (1977) concluded that grass competition strongly reduced growth of *P. radiata* during the first two years after planting and attributed this to competition for soil moisture. However, no direct measures of soil moisture were made although it was observed that grass growth was greatly stimulated by fertilizer. Squire's conclusion that soil moisture limits tree growth is poorly based because the approach did not examine any of the treatment effects on grass growth. Therefore, it is difficult to interpret the results of the trial. Investigation into the factors limiting grass growth should also have been undertaken as part of this research.

It is important to follow the dynamics of both soil moisture and N, particularly in an agroforestry situation where both the dynamics of soil moisture and soil N may be quite different to those in a conventional forestry or pastoral situation. Stands in such situations are more open and soils have a history of higher fertility.

The experiments discussed so far rely on descriptions of competitive interactions as manifested by *performance* and generally have not addressed the *mechanisms* of competition. They are illustrative of the fact that the study of competitive mechanisms has rarely been undertaken. Instead the design and interpretation of experiments so far discussed only reinforce the traditional focus on competitive interactions.

Smethurst and Nambier (1989) examine the interaction between nutrients and water in an experiment where they reduced competition between *P. radiata* and weeds by strip spraying and also by blanket spraying of weeds. This experiment demonstrated that there was strong competition between weeds and *P. radiata* for N and that this was the limiting factor to tree growth and not water. The strong competitive ability of grass was attributed to it having 50 to 100 times the length of roots in the topsoil compared to *P. radiata*.

The design of experiments to examine competition for belowground resources such as N and water is difficult. However, such experiments are necessary if advances in our knowledge of competition are to be made.

1.8 Nitrogen availability

A fundamental difficulty with studying N in forest soils is that the principles of N mineralization, mobilization and availability to plants have been developed mainly through research on agriculture, mineral soils and bacteria. These principles need to be adjusted for forest soils with higher organic matter contents and the presence of fungi (Heal *et al.*, 1982). They may also need special consideration in the agroforestry context.

There has been much conjecture in the literature about the effects of pine species on the availability of N in soils (Stevenson, 1959; Richards, 1962; Fisher and Stone, 1969; McColl *et al.*, 1977; Steele and Percival, 1984; Dyck *et al.*, 1985; Cooper, 1986). Steele and Percival (1984) demonstrated, using N availability indices, that N is less available in soils under *P. radiata* relative to soils under open pasture. Cooper (1986) observed a decline in NO_3^- in runoff waters from a catchment planted in *P. radiata* relative to that from a pasture catchment. He also examined the mechanisms by which *P. radiata* may have reduced N availability in pasture planted with *P. radiata*. Soils from under *P. radiata*, when mixed and incubated under laboratory conditions with pasture soils, did not demonstrate any inhibition of nitrification in pasture soils. The supply of NH_4^+

was the limiting factor. This may come about by reductions in the growth and N content of white clover under *P. radiata* which result in less N being contributed to the soil by white clover N fixation. Therefore, the supply of NH_4^+ may also be consequently reduced (Steele and Percival, 1984).

The importance of N supply versus N availability is reinforced further by Steele and Percival (1984). When N fertilizer was applied there was a pasture response in both open pasture and pasture under pines, but the biggest relative dry matter response occurred under the pine stand (Steele and Percival, 1984). This pasture response to fertilizer under pines raises questions about the effect of *P. radiata* on N availability if, by applying fertilizer, one can alleviate the apparent effect of *P. radiata* on N availability. What is the mechanism by which *P. radiata* influences N supply? Steele and Percival (1984) conclude that *P. radiata* strongly reduces pasture production by direct competition for N. No mechanism for this was suggested.

Although NO_3^- levels in runoff waters decline this does not necessarily mean a decline in N availability and perhaps in nitrifying pasture soils microbial competition for NH_4^+ results in more N being available as NO_3^- (Vitousek and Andariese, 1986). This NO_3^- may either be taken up by plants or it may be lost by leaching or denitrification.

Furthermore, the decline in N availability under *P. radiata* has only been reported at high stockings (200-600 sph) (Steele and Percival, 1984; Cooper, 1986). The consequences of this for agroforestry should not be viewed as negative because the tree pasture system may be more efficient and may retain N in the ecosystem and not lose it in runoff.

1.9 Philosophy of ^{15}N studies

There are two main approaches when using the stable isotope of N - ^{15}N - to study ecosystem processes. In some studies variations in the natural abundance of ^{15}N are used to make inferences about ecosystem processes (Vose, 1980; Vitousek *et al.*, 1989). In other studies, the application of ^{15}N-enriched compounds, mainly fertilizers, has been used to study various aspects of the N cycle, efficiency of N fertilizer applications and the recovery of N fertilizers in various ecosystem components. It has also been used to study the impacts of atmospheric pollution on foliar absorption of N (Bowden *et al.*, 1989; Vose and Swank, 1990). The use of ^{15}N-labelled compounds is now established as a necessary tool for quantifying and understanding N cycling (Binkley and Hart, 1989).

1.9.1 Forestry ^{15}N studies

The stable isotope ^{15}N has most commonly been used to examine the uptake of ^{15}N-labelled fertilizers by the tree crop and the efficiency of fertilizer recovery by the forest ecosystem (Mead, 1971, unpub.; Worsnop and Will, 1980; Heilman *et al.*, 1982b; Melin *et al.*, 1983; Pang, 1985; Nambier and Bowen, 1986; Thomas, 1987, unpub.; Melin and Nommik, 1988; Preston *et al.*, 1990). Application techniques, timing, rate of fertilizer and form of fertilizer have all been studied.

In general, the uptake of fertilizer is low while the losses depend on the ecosystem in question. Competition for ^{15}N-labelled fertilizer either has not been measured, has been ignored or been deliberately excluded (Worsnop and Will, 1980; Heilman *et al.*, 1982b; Pang, 1985; Nambier and Bowen, 1986; Thomas, 1987, unpub.).

Melin *et al.* (1983) report between 3 and 13% recovery by understorey vegetation depending on the form of ^{15}N-labelled N. Preston *et al.* (1990) report recoveries of less than three percent of applied fertilizer in the understorey biomass. In all these studies understorey biomass was small.

1.9.2 Pasture ^{15}N studies

Recovery of ^{15}N in pasture varies widely in the reports in the literature. Steele and Percival (1984) found that recovery of ^{15}N in pasture herbage after 84 days decreased as the rate of urea application was increased. When applying ^{15}N-labelled urea in August, Ledgard *et al.* (1988) obtained 63% recovery in plant tissues after 95 days. In a two-year study of a grass ley Hansson and Pettersson (1989) calculated a crop recovery of 92%. Bristow *et al.* (1987) report a recovery of 54.7% of ^{15}N double-labelled NH_4NO_3 in pasture herbage after 370 days. Watson (1987) reported recoveries in herbage ranging from 31 to 53% with between 15 and 24% in the roots after a seven-week pot trial. Whitehead and Dawson (1984) found that recovery of ^{15}N double-labelled NH_4NO_3 in pasture herbage after 184 days was 60 and 62% in irrigated and unirrigated pastures respectively.

Overall comparisons of fertilizer recovery are difficult to make due to inherent differences in the experimental design. Recoveries of ^{15}N fertilizer in the crop biomass are higher in agricultural studies than in forestry studies while immobilization of ^{15}N fertilizer in forest soils is higher than in agricultural soils. These differences are apparently due to inherent differences in crop demands, soil fertility and the N cycle.

1.10 The effect of grazing on tree growth

It is often reported, but still unproven, that the increased growth of trees in grazed pastures is in part due to the increased rate of nutrient cycling, especially N, through the dung and urine from grazing animals. Alternatively, the increase could be due to the generally higher fertility of the sites. The latter is more likely as Thomas (1987, unpub.) did not find any additional benefit to tree growth using split applications of N compared to a single dressing. However, the interaction between frequency and magnitude of the returns of N in a grazed agroforest could have a significant effect on tree growth compared with the split application of N fertilizer (Thomas, 1987, unpub.) and may cause a growth response not seen by Thomas.

Furthermore, another possible explanation of the increased growth of *P. radiata* in grazed pastures is a reduction in allocation of photosynthate to belowground organs by reducing its reliance on mycorrhizal associations (Alexander and Fairly, 1982; Bowen, 1984).

Steele and Percival (1984), using ^{15}N-labelled urea, found that in a stand of eight-year-old *P. radiata* at 400 sph after 84 days, 34% of a single application of 100 kg/N ha was recovered in the pasture. Of the total quantity applied, 26% was left in the soil. By difference it was concluded that up to 40% of the applied N might have been taken up by *P. radiata*. Unfortunately the study was not designed to measure directly the recovery of ^{15}N by *P. radiata*.

They also found ^{15}N recovery in pasture and soils decreased as tree stocking increased but a relatively greater pasture response to N fertilizer occurred with increasing stocking. Responses to N by pasture growing under pines have also been reported by Hart *et al.* (1970) and Teare *et al.* (1987). Steele and Percival conclude that *P. radiata* strongly reduces pasture production by direct competition for N and that this competition could be reduced by applying N fertilizer because pasture responded strongly to N.

Given the usual low uptake of ^{15}N by trees, and especially that of *P. radiata* (Nambier and Bowen, 1986; Thomas, 1987, unpub.), it is important that the high tree uptake suggested by Steele and Percival (1984) be examined. The highest reported uptake of ^{15}N in forest species is 44% for calcium nitrate (Melin and Nommik, 1988) for a 50-year-old mixed stand of Scots pine and Norway spruce with a shrub understorey on a podzol soil. Uptake of ^{15}N-labelled urea fertilizer was 20% in the same study. The implications of these observations are that uptake and also ecosystem recovery (Melin and Nommik, 1988) may be directly affected by the form of applied N and the relative fertility of the site in question.

The studies of Nambier and Bowen (1986) and Thomas (1987, unpub.) demonstrate that there is insufficient evidence to support Steele and Percival's (1984) claim that *P. radiata* takes up large quantities of ^{15}N. For their conclusion to be valid it would be necessary to assume that the animals grazing under trees had a large beneficial effect on *P. radiata* growth and N uptake.

The importance of studying the movement of ^{15}N in the whole ecosystem is seen from the example of Steele and Percival's study. In this study the uptake of ^{15}N by pasture and *P. radiata* and recovery in soil will be assessed at different levels of competition between trees and pasture to determine the extent of competition for N and the likely benefits of grazing to tree growth.

Chapter Two

Materials and methods

2.1 Overview

The objective of the field trial was to examine the outcome and some of the competitive mechanisms between *P. radiata* and pasture for N and soil moisture.

The factors examined were:

- monthly addition of 30 kg N/ha versus no additional N,
- manipulation of the level of pasture competition by spraying and simulated-grazing to give three levels of pasture competition.

A single application of labelled $^{15}NH_4^+$ fertilizer was used so that the fate of, and competition for, N could be assessed at a time of rapid tree and pasture growth.

Six treatments in the 3 x 2 factorial were:

- rank-no-N,
- rank-plus-N,
- simulated-grazing (return of nutrients removed in clippings)-no-N,
- simulated-grazing (return of nutrients removed in clippings)-plus-N,
- spraying-no-N, and,
- spraying-plus-N.

These were established in autumn 1988 to allow for the conditioning of the system to increased levels of N before the ^{15}N was applied in spring. In all, 11 monthly applications of N were made, one of which was labelled with ^{15}N.

Within the simulated-grazing-plus-N treatment both ^{15}N-labelled NH_4^+ and NO_3^- were used to examine whether there was a preference by *P. radiata* or pasture for the form of applied N fertilizer.

Growth and biomass and N uptake by *P. radiata* were assessed after one year to examine the effect of pasture competition and monthly additions of N. The effects of treatments on pasture production and N uptake were also examined.

Nitrogen mineralization using *in situ* incubations was also quantified to assess the effects of the treatments on N availability and N uptake. Soil moisture content was monitored using weekly neutron moisture meter readings to assess the effects of treatments on the availability and dynamics of soil moisture.

Furthermore, within the simulated-grazing treatment a trenching experiment was established to exclude *P. radiata* roots and so determine their impact on pasture growth and uptake of N and ^{15}N.

2.2 Site history, climate, vegetation and soils

The trial was located S.W. of Rangiora, 35 km from Christchurch, at latitude 43° 19' S and longitude 172° 34' E. The trial area was part of a block of land once used for *P. radiata* seedling production by the New Zealand Forest Service, Rangiora Nursery. It was retired from production in 1970 because of loss of soil structure, and was placed under a grass fallow for restoration. In 1984, about one hectare was planted at 400 stems per hectare *P. radiata* for a post-planting weedicide trial (Balneaves, 1987). This trial was abandoned in 1986 and the understorey was left to revert to a cocksfoot-dominated rough pasture.

In preparation for this trial the site was tractor mowed in August 1987 and the silage was removed from the site by hand. To improve the cocksfoot pasture the site was oversown with 10 kg/ha of ryegrass and 2 kg/ha white clover. Forty kilograms P/ha were applied as superphosphate resulting in the establishment of a vigorous sward dominated by white clover, cocksfoot and ryegrass.

The soils of the site are classified as a Templeton silt loam. The soil is developed on fine alluvial sediments and is medium- to free-draining with a moderate capacity to retain moisture (Kear *et al.*, 1967).

Climate data for the study area were obtained from the meteorological site at the Forest Research Nursery at Rangiora, which is approximately one kilometre from the field trial. The climate of the area is similar to that of the Canterbury plains. Hot dry north-west foehn winds are common during the spring and summer and are responsible for periods of no or low rainfall. These winds greatly reduce relative humidity. For example in October 1988, average daily relative humidity was 49% compared with the long-term average of 66% (Fig. 2.1).

The long-term average (1965-1980) rainfall of 702 mm (range 372-988 mm) is spread evenly throughout the year (Fig. 2.2), although periods of 30 consecutive days of less than one millimetre of rainfall are common (McGann, 1983). However, for the period of the experiment, April 1988 to April 1989, rainfall was only 59% or 415 mm of the long-term average. During this time there were 11 periods of seven days duration or longer when less than or equal to 0.1 mm of precipitation fell. Six of these occurred during the winter and spring, thus aggravating the summer drought.

Weekly mean air and soil temperatures in the top 10 cm for the period January 1987 to May 1989 measured at 3 p.m. for the Rangiora nursery meterological site are shown in Figures 2.3a and 2.3b. The winter of 1988 was milder than the previous year and both air and soil temperatures were generally warmer than in the previous year.

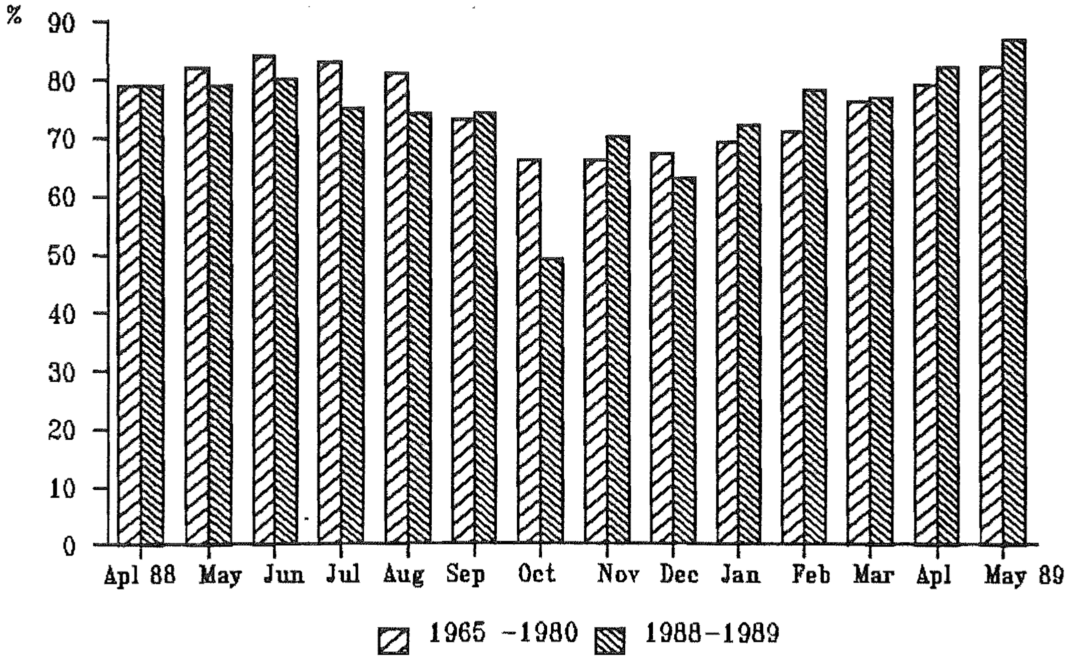

Figure 2.1 Average monthly relative humidity at 9.00 a.m. (1965-80) compared to that for April 1988-May 1989.

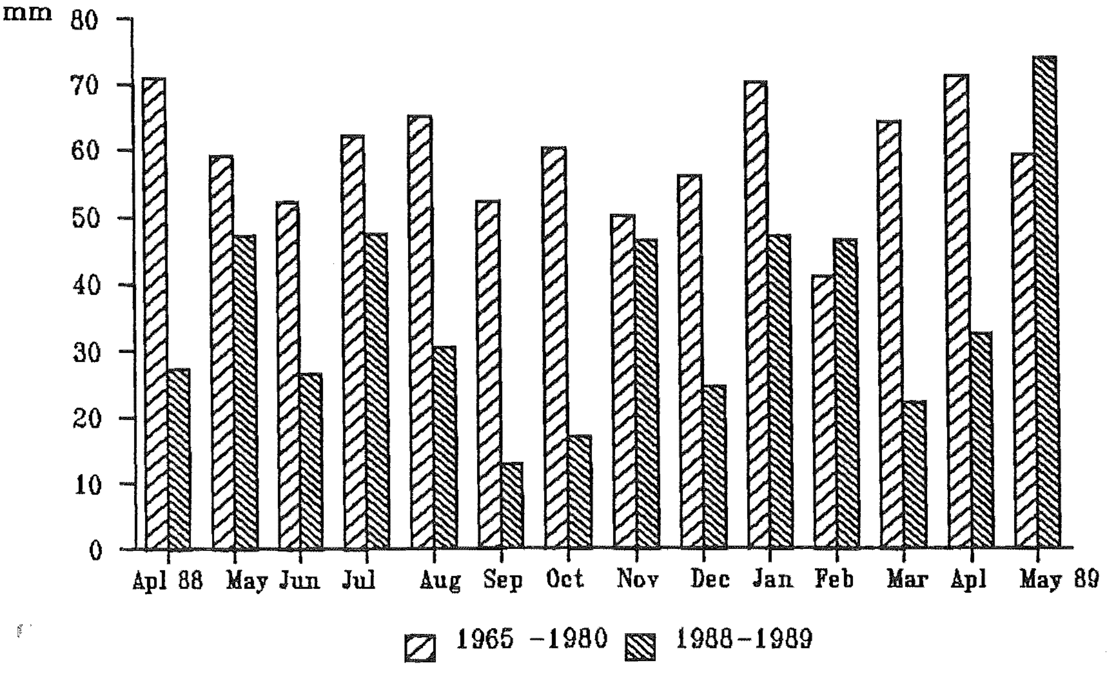

Figure 2.2 Average monthly rainfall (1965-80) compared to that for April 1988-May 1989.

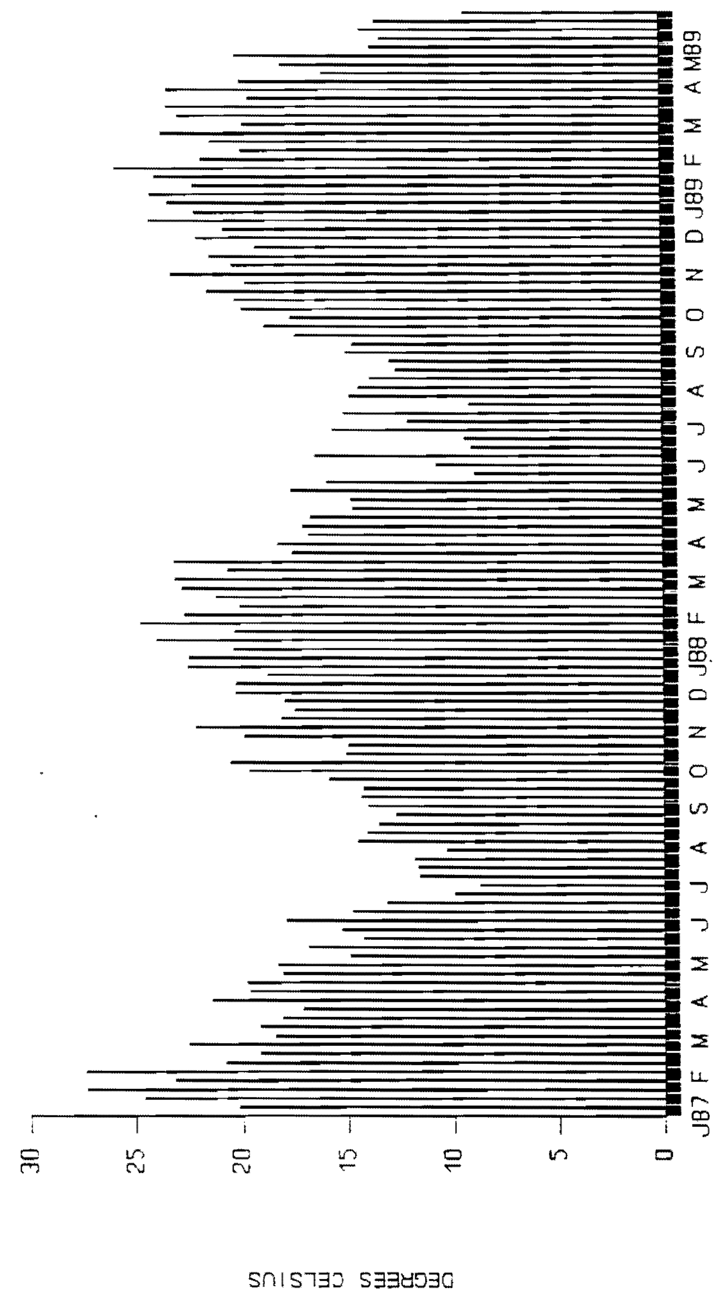

Figure 2.3a Weekly mean air temperature for January 1987-May 1989.

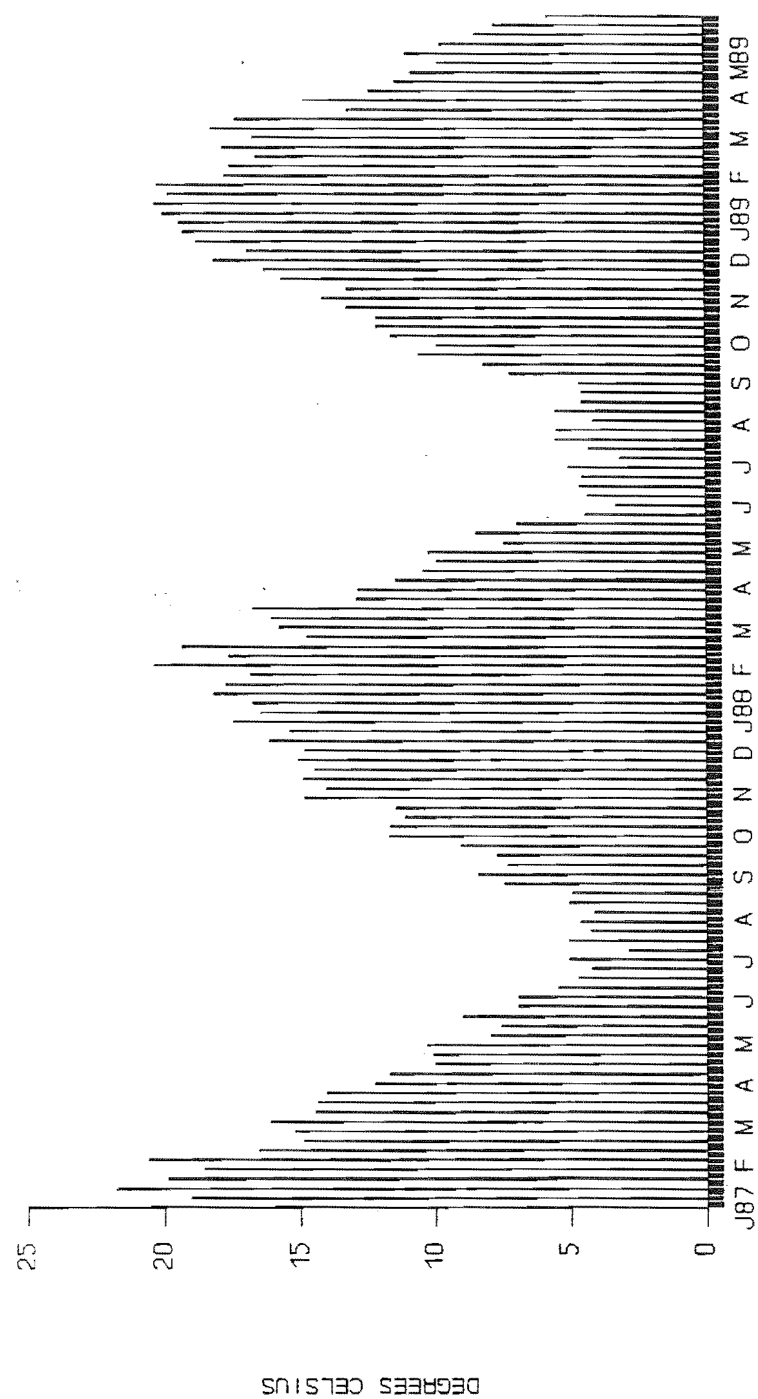

Figure 2.3b Weekly mean soil temperature in top 10 cm of soil for January 1987-May 1989.

2.3 Experimental design

The main trial was laid out as a 3 x 2 factorial in pasture competition and N fertilizer. The three levels of pasture competition were:

- rank pasture,
- simulated-grazing by mowing and removal of clippings and return of some of these nutrients removed in the clippings as fertilizer additions,
- kill-spraying using Roundup[1] (active ingredient glyphosate) to remove all competing vegetation.

The second factor was the monthly addition of N applied at two levels - 0 and 30 kg N/ha month. In February 1988 the six treatments[2] were laid out as a completely randomized design with four replicates. A separate experiment, to examine the difference in uptake of ^{15}N-labelled NH_4^+ and ^{15}N-labelled NO_3^-, was established in four extra replicates of the simulated-grazing-plus-N treatment.

The data were analyzed either by analysis of variance or by analysis of covariance. The homogeneity of regression slopes between treatments for each covariate and measurement variable was tested.

Orthogonal contrasts were made in the main experiment but the three single degree of freedom contrasts used in the analysis of the ^{15}N data were not orthogonal but were used as they are the sensible contrasts that are of interest in this experiment.

For those variables where measurements were made on several sampling dates, the effects of the experimental treatments were tested using repeated measures analysis of variance (Winer, 1971; Moser *et al.*, 1990). Where the test of sphericity was satisfied the univariate statistics were used otherwise the Wilks Lambda multivariate test was used to examine within-subject effects (time) and the interaction of time and treatment effects. If the sphericity test could not be performed due to missing cases, multivariate statistics were used. If multivariate tests could not be performed by SAS, then the significance levels for F tests

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1 Manufactured by Monsanto Corp.

2 The six treatments were:
- rank-plus-N
- rank-no-N
- simulated-grazing (return of nutrients removed in clippings) -plus-N
- simulated-grazing (return of nutrients removed in clippings) -no-N
- spraying-plus-N
- spraying-no-N.

adjusted by the Huynh and Feldts estimator were used. Caution was used in interpreting the univariate tests whenever the sphericity test was rejected ($P < 0.0001$).

Significant time x treatment interactions were plotted. Least significant differences were included on some figures as a guide to variability (Andrews *et al.*, 1980).

2.4 Experimental treatments

2.4.1 Competition experiments

Plots assigned to the rank treatment were last mowed on 22 February 1988 and simulated-grazing plots were first harvested on 23 March. Plots in the spraying treatment were sprayed on 28 April with Roundup (15 kg/ha) and Pulse[3] as penetrant. Any further weed growth was removed with periodic spot spraying and Versatill[4] (1 kg/ha) was used to remove flatweeds and clovers that persisted.

In the simulated-grazing treatment the whole plot, excluding the small pasture production plots, was mowed with a rotary mower to a height of three centimetres and clippings were removed.

2.4.2 Nitrogen additions

Nitrogen was applied at the rate of zero and 30-32 kg N/ha/month. Due to difficulties encountered in purchasing NH_4NO_3 at the start of the experiment it was only possible for NH_4NO_3 to be used on half the application dates (Appendix 2.1a) when N was applied as 15 kg/ha as NH_4^+ and 15 kg/ha NO_3^-. Therefore, on alternate dates, a mixture of calcium ammonium nitrate and KNO_3 was used and N was applied as 10 kg/ha as NH_4^+ and 22 kg/ha as NO_3^-. The first application of 30 kg N/ha was made on 5 May 1988. The drought conditions experienced in November 1988 saw the fertilizer applied during that month remain on the surface for some time. This was considered undesirable and due to continuing drought conditions the December 1988 and January 1989 additions were omitted and only 11 applications were made in total. On average, 56% of the N was applied as NO_3^--N. And each plot also received 128 kg K/ha and 69 kg Ca/ha from the monthly addition of N.

In addition, the simulated-grazing-plus-N plots received an average of 104 kg N/ha (Appendix 2.1b).

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[3] Manufactured by Monsanto Corp.

[4] Manufactured by Ivon Watkins-Dow Ltd.

2.4.3 Addition of ^{15}N

Labelled N was applied in spring on 12 September 1988 to the central tree in three of the four replicate plots in the plus-N treatments. This treatment consisted of N at the rate of 15 kg N/ha as ^{15}N-labelled $(NH_4)_2SO_4$ (11.97 atoms % ^{15}N) and 15 kg N/ha as unlabelled KNO_3. This was applied to unconfined 1.9-m-radius plots. The equivalent of 2.47 mm of water was used to apply the ^{15}N in solution (Fig. 2.4). For the comparison of ^{15}N-labelled NH_4^+ with NO_3^- within the simulated-grazing-plus-N treatment, three plots received N at the rate of 15 kg N/ha as ^{15}N-labelled KNO_3 (11.18 atom% ^{15}N) and 15 kg N/ha as unlabelled $(NH_4)_2SO_4$. Labelled N represents seven percent of the total N added for the grazing treatment, and nine percent of the total N added to rank and sprayed treatments.

2.5 Measurement of experimental variables

2.5.1 Pasture production

To measure pasture production two 4 m^2 plots in each replicate of the grazing and grazing-plus-N treatments were established on 17 February 1988. These were first clipped on 27 February, 47 days after they were last mowed by tractor. This simulated-grazing was repeated at Days 54, 120, 150, 184, 198, 220, 248, 283, 325, and 419. The centre of each plot was located midway on diagonal lines between the central tree and corner trees of the plots (Fig. 2.5). Initially pasture production was measured by clipping the plots to a height of three centimetres with a reel mower. Plot size was reduced to 0.25 m^2 from 26 September onwards to reduce the labour involved. These were randomly located within the original 4 m^2 plots.

2.5.2 Return of nutrients removed in clippings from grazing plots

It was impractical to determine nutrient concentrations quickly after each harvest, therefore the quantity of nutrients to be returned to plots in the simulated-grazing treatment was estimated from actual weight of dry matter removed at each harvest and the concentrations of N, P, K, and Mg determined from samples collected at a pre-treatment harvest (Appendices 2.2a and 2.2b). Urea was used for the addition of N removed in clipped pasture, unlike the monthly addition of N which involved application of N as NH_4^+-N and NO_3^--N. This distinction was made because urea is more representative of the form of N returned by animals. Phosphorus, K, and Mg were returned as superphosphate, KCl and $MgSO_4$ fertilizers. The only Ca returned was added in the superphosphate assuming a 20% Ca content (During, 1984).

Only 80% of the estimated quantity of nutrients removed in the clippings was returned (Quinn, 1982) (Appendix 2.3). The return of N removed in the simulated-grazing-plus-N treatment was 23% of the total N added. Nutrients removed in clippings were returned on 10 October 1988, 28 November 1988, and 2 February 1989.

Figure 2.4 Application of ^{15}N solution to plots.

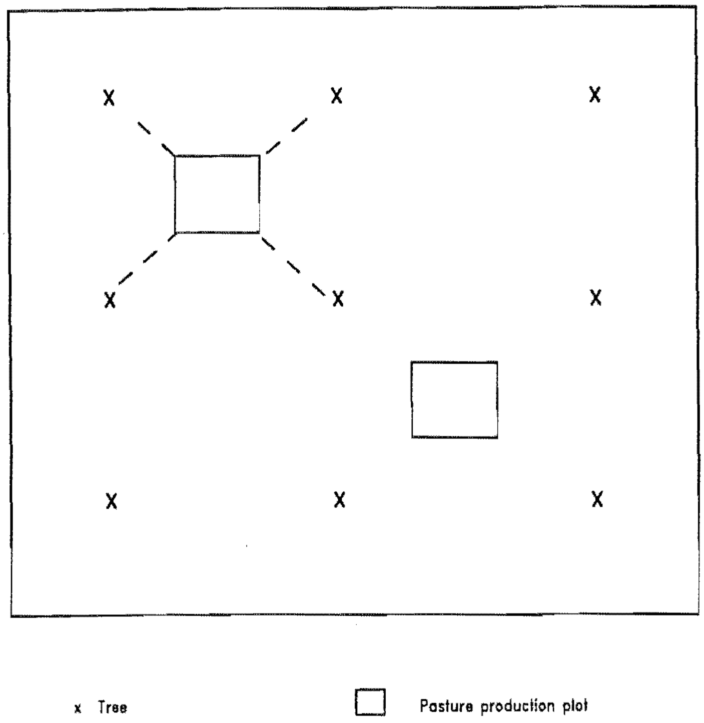


Figure 2.5 The location of pasture-production plots within main plots.

2.5.3 ^{15}N uptake by pasture in simulated-grazing treatment

The ^{15}N-treated areas were first harvested on 26 September 1988, 14 days after ^{15}N application. A two-metre-radius aluminium ring was positioned with the tree at its centre. It was planned to remove all material from inside the area delineated by the ring, the area to which ^{15}N-fertilizer was applied. It was not possible to collect all material on 26 September or when the plots were next harvested (10 October, 28 days after application), because of the height and quantity of pasture. Instead, on these two occasions when pasture cover was relatively uniform, a single randomly located 0.25 m^2 plot inside the ring was clipped to a height of three centimetres. The rest of the plot was mowed with a rotary mower to a height of three centimetres and discarded. Entire plots (11.34 m^2) were completely harvested again at 50, 77, 113, and 154 days from application. On these occasions a reel mower was used to clip the plots to a height of three centimetres. Areas under the tree that could not be mowed were clipped by hand.

2.5.4 Tree measurements

Root collar at 10 cm aboveground level was marked on trees on 28 January 1989. The trees were then measured for diameter (to the nearest millimetre) and height (to the nearest 0.05 m) at monthly intervals.

2.5.5 Foliage sampling

In April 1988 the crown of the central tree was divided into three sectors: lower, mid, and upper which corresponded to ages of two years or older, one-year-old and current year respectively (Fig. 2.6a). One whorl of branches in each sector was tagged. These branches were subdivided into different ages of foliage and from each age class two to four fascicles per branch, approximately 30 fascicles per whorl, were collected and counted each month. In September, when height growth resumed, the first major new whorl of branches was tagged and needle samples were also subsequently taken from these parts of the tree and are referred to as uppermost samples. For most purposes samples from the lower and mid crown positions were bulked and referred to as lower crown samples. Samples were dried at 70°C to constant weight and weighed to the nearest milligram; mean needle weights were then calculated. Samples of senescent needles were collected on 31 May 1988 and again on 8 March 1989. These were taken from the mid crown position.

2.6 Whole tree biomass harvest

The 26 trees were harvested for biomass estimates over a period of 17 days between 2 May and 19 May 1989. The total root systems of 20 of these trees were excavated. Individual trees were divided into six needle, two wood, two bark, and two branch classes, and buds, fine roots, large roots and stump samples.

2.6.1 Harvest procedure

A tarpaulin was placed beneath the tree to be felled and, after felling, the crown was divided into the four zones used for sampling needles (Section 2.5.5). Once removed, the whorls of branches were bulked by zones and the lower and mid crown positions were further bulked and are referred to as lower crown samples (Fig. 2.6b). From each bulked sample, four to five branches were randomly taken as a subsample for detailed dissection by age class (current, one-, two-, three- and four-year-old into needles and branches). Current developing buds were removed from branches and treated as a separate sample. Branches were kept in the coolstore overnight if necessary and typically remained there fewer than 24 hours before being processed.

The remaining branches in the lower, upper and uppermost crown bulk samples were divided by age class and these bulk samples of unsorted needles and branches were weighed fresh.

The stem was dissected into annual height growth sections and the fresh weight recorded. Three centimetre disks were taken from each section and the complete terminal shoot of the main stem was taken as a sample. In addition, a disk was also taken from the base of the stem.

The disks were dissected into bark, current increment and older wood. Subsamples were oven-dried at 70°C in a forced draught oven for determination

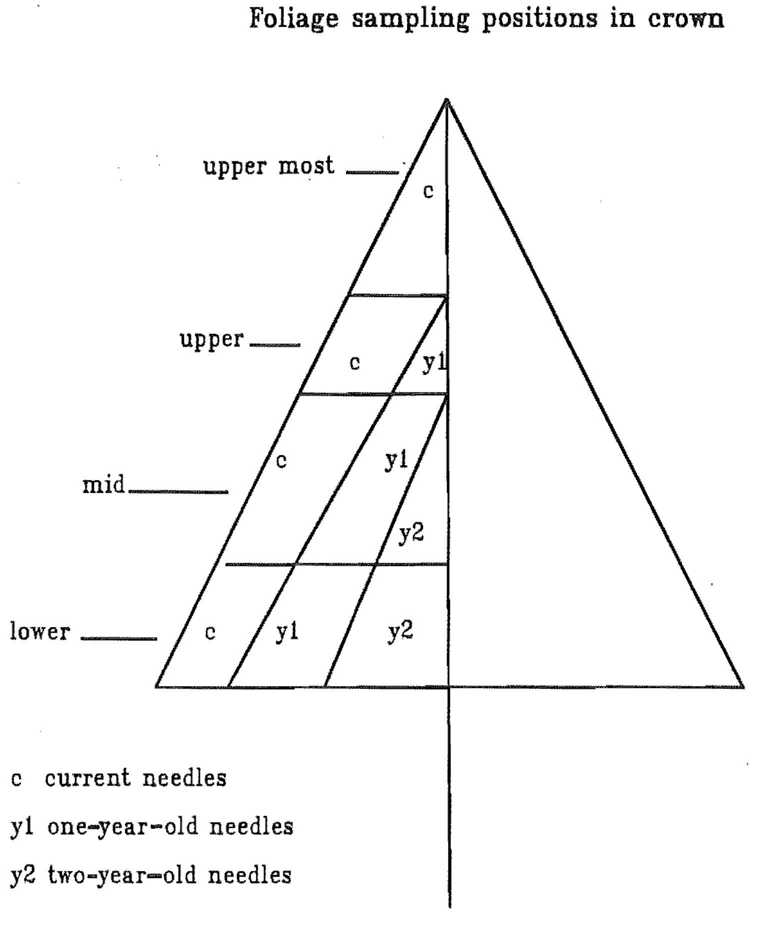


Figure 2.6a Location of foliage samples.

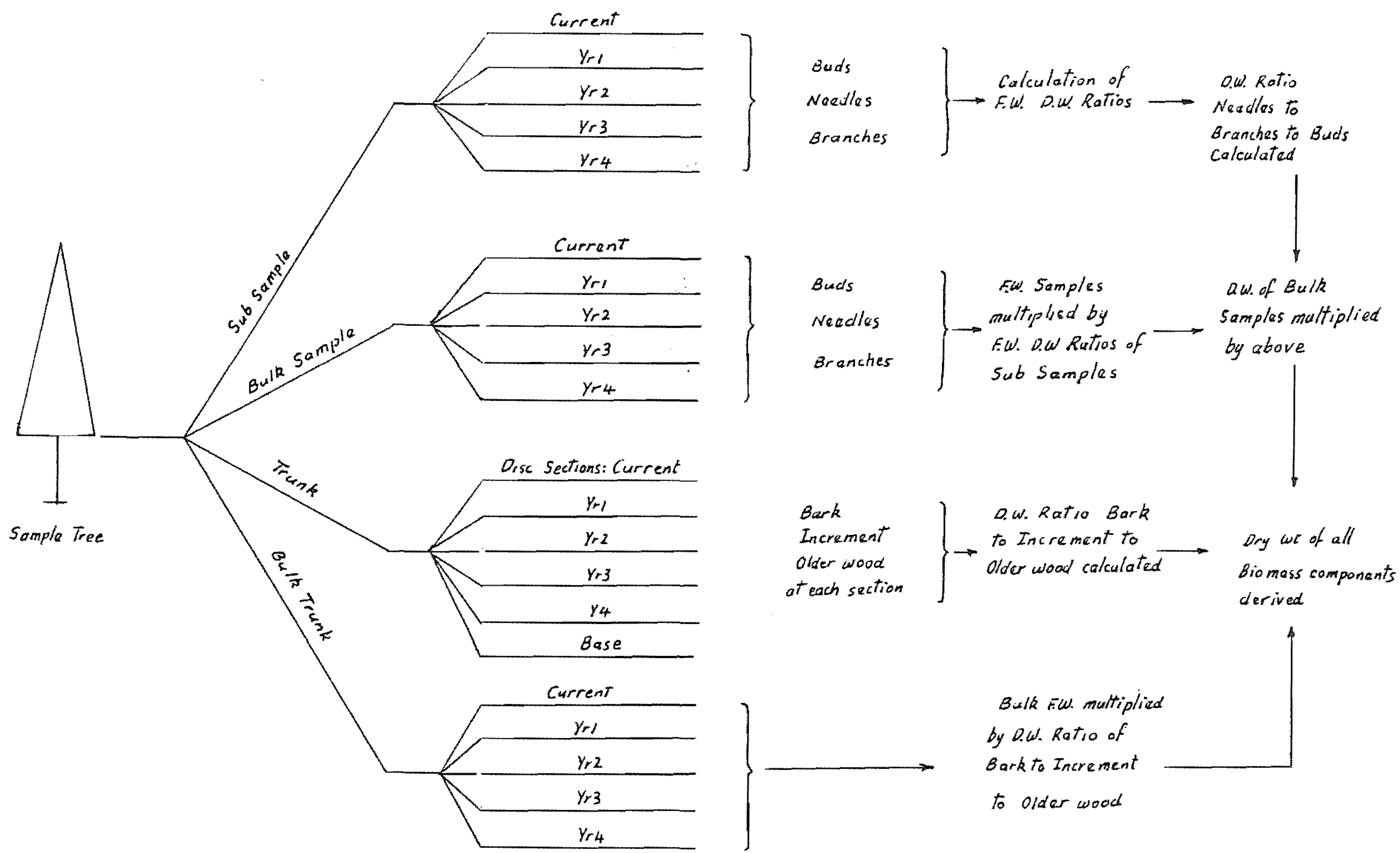


Figure 2.6b Sampling process for deriving oven-dry weight of the biomass components.

of moisture content. Oven-dry samples were weighed to the nearest 0.1 g when samples did not decrease in weight over a 24-hour period. Total oven-dry weight by components was estimated from total green weight of the components and from the ratio of dry to green weights in the subsample (Fig. 2.6b).

2.6.2 Herbage and stubble collection

An aluminium ring with radius two metres was placed around the stump. Hand shears were used to clip herbage and stubble to ground level inside an area 1.9-m-radius from the stem centre, leaving a 10-cm-wide outer boundary. Clippings were weighed and oven-dried. Surface litter from underneath the tree was then removed by scratching, with a garden leaf rake, weighed, well mixed and a subsample taken for oven-drying.

2.6.3 Soil sampling

After the litter layer had been removed, four randomly located soil pits, 0.0306 m^2 in area were excavated from 0-10 and 10-20 cm soil depth. They were bulked by depth. Pits were relocated if large tree roots interfered with their excavation. Bulked soil samples were weighed fresh and stored at 3°C until being further processed. Soil samples were collected from 20-60 cm in eight of the ^{15}N-fertilized plots after the root systems had been excavated.

Soil bulk density for the 0-10, 10-20 and 20-60 cm soil depth was determined prior to the final harvesting of the trees. Four randomly located pits, 0.0306 m^2 in area, were carefully excavated from 0-10 and 10-20 cm, and two 6.5 cm diameter cores were taken from 20-60 cm soil depth. Subsamples were oven-dried at 105°C for 48 hours. Oven-dry weights were adjusted by the proportion of less than two millimetre fraction determined for cores taken during the installation of the neutron moisture meter access tubes. In this way bulk density for 0-10 cm soil depth was calculated for each plot and a pooled bulk density estimate was used for 10-20 and 20-60 cm soil depths. All soil data were expressed on an oven-dry basis.

The bulk soil samples were well mixed by hand; small clods were crumbed. Large fragments of pine roots, pasture roots and stubble were removed and set aside for later processing (Sections 2.6.5 and 2.6.6). A subsample of 1-2 kg soil was taken for total N analysis. In the ^{15}N-fertilized plots the subsamples were sieved (less than two millimetre) and three 10 g subsamples were taken for moisture factor determination for the fresh soils. Approximately half the remaining sample was air-dried before being ground in a Rock Lab. ring grinder for five minutes. Moisture factors were determined for the finely ground subsamples. The other portion of the fresh subsample was used for KCl extractions to obtain mineral N (Section 2.9.2). The remainder of the bulk soil sample was retained for pine and pasture root biomass determinations (Section 2.6.6).

2.6.4 Sampling of tree root systems and stump

Using grubbers, picks and shovels, large diameter lateral roots were traced out from the stump until their ends were exposed. The top 10 cm of soil was excavated from within a 1.9 m radius of the stump centre and all tree roots were collected as they were exposed. Any roots that had extended outside this radius were also collected although this was uncommon. Once this had been done lateral roots still attached to the stump were removed and any sinker-type roots were followed down. The stump and taproots were excavated by digging a large pit about 1.5 x 1.5 m^2 and up to two metres deep.

2.6.5 Pasture and pine fine root biomass

The collection and initial processing of root samples was described in Section 2.6.3. It was not possible to separate live and dead pasture roots. Separation of live and dead pine roots was on the basis of their appearance and the integrity of their cortex. Differentiation by colour alone was difficult due to a decline in their condition during storage. While it is possible that a small amount of fine roots was lost in the subsample taken for soil analysis this would have resulted in only a small underestimate of fine root biomass.

2.6.6 Root recovery process

The sample was washed over a four millimetre sieve with successive portions being washed. Using tweezers, roots were picked from the sieve and sorted into one of the following categories: pasture roots and stubble, dead pine roots, live pine roots less than one millimetre diameter (referred to as fine pine roots), and large pine roots. This process took between three and eight hours per sample depending on the quantity of pasture roots. Roots were dried to a constant weight at 70°C in a forced air oven.

2.6.7 Preparation of biomass samples for nitrogen analysis

Once needle and branch samples had been oven-dried, needle samples were bulked by position for each tree. Current branch samples were combined as were older branch samples. Large samples of needles, branches, and wood were first ground to pass through a four millimetre mesh and then were well mixed before being subsampled and ground in a Wiley mill with one millimetre mesh. Samples were then further subsampled before being ground in the Rock Labs ring grinder.

Root and stump samples were first ground using a Yeoman hammer mill; stumps were first cut into small pieces using a chainsaw and subsampled. After subsampling the procedure was the same as for other samples.

To improve the reproducibility of ^{15}N analysis, all samples were ground for at least five minutes (10 minutes for woody samples) in the ring grinder. To avoid cross-contamination, acid-washed sand was ground between ^{15}N-enriched samples and ethanol and wire wool were used to remove sticky sample residues.

2.7 Trenching experiment

The trenching experiment was designed to examine the effects of *P. radiata* roots on ^{15}N uptake of pasture. It consisted of three replicate pairs of trenched and untrenched plots in both the simulated-grazing-plus-N and simulated-grazing-no-N treatments. The trenched plots were located between two trees not used for intensive measurements and were 3 x 3 m^2 in area and were established over a period of seven days (25 to 31 August 1988), 12 to 18 days before the application of ^{15}N-labelled fertilizer. A ditchwitch trencher was used to make a 10-cm-wide trench, 80 to 90-cm-deep continuous trench around the perimeter of the plot. These trenches were lined with polythene and carefully backfilled. The actual sample plots were 0.25 m^2 in area (Fig. 2.7) with a 10-cm-wide treated surround giving a total plot area of 0.36 m^2.

Each pair of 0.36 m^2 plots in the simulated-grazing-plus-N treatment received ^{15}N-$(NH_4)_2SO_4$ (11.97 atoms %^{15}N) applied at a rate of 15 kg N/ha plus 15 kg N/ha as unlabelled KNO_3 on 13 September 1988. The equivalent of 2.47 ml of rainfall was used to water the ^{15}N-labelled fertilizer on in solution. Plots in the simulated-grazing-plus-no-N also received this quantity of water.

Location of sample plots in trenching experiment

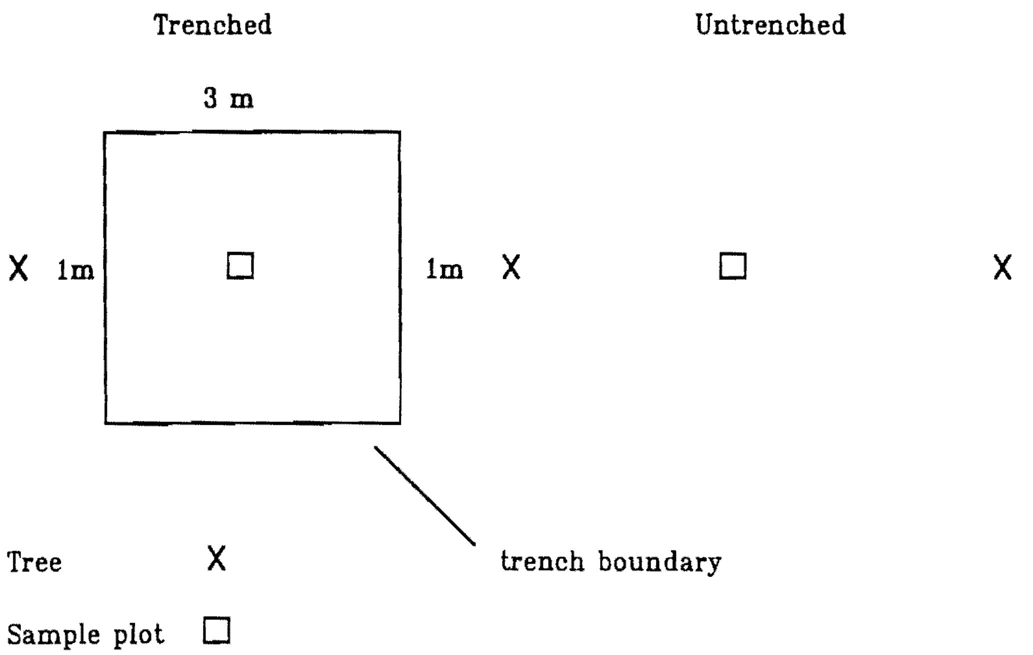


Figure 2.7 Location of sample plots in trenching experiment.

Plots were first harvested on the 26 September, 13 days after ^{15}N application. A 0.36 m^2 template with a central 0.25 m^2 cut-out was placed over the 0.36 m^2 plot. In this fashion the central 0.25 m^2 of the plot was clipped to a height of three centimetres. Plots were harvested again on Days 27, 49, 76, 112, 153, 248, and 382 after ^{15}N application.

On 29 September 1989 plots were destructively sampled. Herbage was clipped to ground level and a pit 0.03 m^2 in area was excavated to 10 cm; all soil and pasture and pine roots were removed. The pits were further excavated to a depth of 20 cm and a sample was taken from 20-50 cm depth using a 6.5-cm-diameter corer.

Soil samples were kept in the coolstore until they were processed. Samples were broken up into crumbs and well mixed. A subsample of approximately one kilogram was taken from each sample and partially air-dried before sieving. A two millimetre sieve was used to remove the greater than two millimetre fraction. Pasture roots or live and dead pine roots caught in the sieve were returned to the sieved soil and air-dried before being ground in a Christy & Norris eight inch laboratory mill. From this fraction, a 100 g subsample was ground in the ring grinder for five minutes.

2.8 Nitrogen mineralization experiment

A modified buried plastic bag method (Westermann and Crothers 1980; Pastor *et al.*, 1984) was used to assess N availability under field conditions. This method is sensitive to on-site temperature regimes and may also reflect on-site soil moisture levels if soil moisture conditions throughout the incubation do not change significantly from initial conditions. This method was chosen because a preliminary attempt using *in situ* cores (Raison *et al.*, 1987) was unsuccessful due to the weakly developed structure of the soil profile.

Two pairs of intact cores 15 cm long, one collected within a radius of one metre of the stem and the other between one and 2.5 m radius, were collected from two of the four replicates of each treatment using a 6.5 cm corer each month starting in April 1988. Each core was divided into 0-5 and 5-15 cm segments and placed in plastic bags which were sealed. One core in each pair was returned to its hole for field incubation.

The two segments from the other core were returned to the laboratory for extraction the next day. Cores were stored overnight at 3°C. At each collection, cores from the previous month's incubation were collected. The first set of cores was established on 21 April 1988 and incubated in the field for 30 days. Successive field incubations ran for 27 days for April, 28 days for May, 32 days for June, 24 days for July, 28 days for August, 28 days for September, 28 days for October, 28 days for November, 35 days for December, 28 days for January, 36 days for February, 27 days for March, and 21 days for April 1989.

2.8.1 Processing of cores

Cores were broken into small crumbs by hand and a five gram subsample at field moisture content was shaken with 50 ml of 1 M KCl for one hour. Extracts were filtered through Whatman No. 2 filter paper, bottled and kept in the fridge at 3°C until being analyzed. The amount of NH_4^+ and NO_3^- was determined within seven days of extraction. Blanks of KCl were processed along with samples. The moisture factor was determined by oven-drying 10 g subsamples, for 48 hours at 105°C.

Ammonium and NO_3^- in 1 M KCl extracts were determined using automated colorimetric analysis. Ammonium was determined using the indophenol reaction with nitroprusside catalyst (Searle, 1984) with the absorbance measured at 660 μm. Nitrate was reduced with hydrazine and absorbance was measured at 520 μm (Kamphake *et al.*, 1967). Any nitrite present was included in this value.

Duplicate standards were run every eight samples with the analysis of individual samples being corrected for drift. Approximately eight samples were analyzed in duplicate per run to test for reproducibility. The coefficient of variation was always less than four percent.

Net mineralization of N was calculated as the sum of NH_4^+ and NO_3^- in 1 M KCl soil extracts at the end of the incubation period minus the initial amount of NH_4^+ and NO_3^- present before incubation.

2.9 Total nitrogen and ^{15}N-labelled nitrogen of ^{15}N-fertilized trees

2.9.1 Mass spectrometry

Total N and ^{15}N analyses of ^{15}N-fertilized trees were initially performed by S. Hadfield and latterly by G. Ridgen of the Soil Science Department, Lincoln University, using direct combustion mass spectrometry. A fully automated system incorporating a Europa scientific Roboprep N analyzer fitted with gas chromatograph interfaced to a Europa Scientific Tracer mass stable isotope mass spectrometer was used for total N and ^{15}N sample analyses.

The basic principles of this automated method of ^{15}N analysis have been discussed by Harris and Paul (1989) and Schepers *et al.* (1989). The procedures used differed in the source of oxygen and hydrogen, the temperature of the oxidation chamber (approximately 1000°C), and chamber temperature at ignition (approximately 2000°C), size of capillary tubing used to connect N analyzer and mass spectrometer (R. Sherlock, Soil Science Department, Lincoln University, pers. comm.). Samples were weighed on an AND model ER182A microbalance. For plant and soil samples 5-10 mg and 30-50 mg were used respectively. For soil extracts, concentrated distillates containing approximately 2 g N/ℓ were used. All instruments were controlled from an IBM clone personal computer which was used to collect and process data using software supplied by Europa Scientific.

Internal standards were included in each batch of samples (Appendix 2.4a). Prepared standards of known enrichments were also used.

2.9.2 Preparation of 1 M KCl extracts of soil for ^{15}N analysis

Recovery of ^{15}N in soil was assessed at 14 and 154 days after the application of ^{15}N-labelled fertilizer and again at the end of the experiment. At each occasion a bulked sample from 20 cores, 2.5 cm diameter and 10 cm deep, was randomly taken from within the area that received ^{15}N. After the fresh samples were sieved through a two millimetre sieve and mixed they were split into two subsamples of approximately 600 g. One was air-dried in preparation for total N analysis and ^{15}N determination and the other was used for determining mineral N.

Mineral N was determined in triplicate by adding 100 ml of 1 M KCl to 10 g subsamples weighed into glass jars. These were sealed and shaken end over end for one hour. The resultant suspension was briefly allowed to settle (standing time was 10 to 20 minutes) and then the supernatant was filtered through a Whatman No. 2 filter paper. Filtered samples were refrigerated until being analyzed. Triplicate 10 g subsamples were also taken for moisture factor determination.

2.9.3 Distillation procedure

Ammonium and NO_3^- were determined on 10 ml aliquots of each replicate using MgO and Devardas alloy as catalysts for NH_4^+ and NO_3^- respectively (Keeney and Nelson, 1982); distillates were collected in five millilitres of 2% boric acid indicator solution and were titrated with standardized 0.005 N sulphuric acid (Keeney and Nelson, 1982). Separate distillations were required for the ^{15}N analyses; two to three 20 ml aliquots being necessary. These distillates were collected in 1.5 ml of 25 mM sulphuric acid and acidified with one millilitre of 0.1 N sulphuric acid (Buresh *et al.*, 1982).

All replicates were combined to give one ^{15}N sample for each soil sample. If, after combining, the collective sample contained less than 2 g N/ℓ, an appropriate amount of $(NH_4)_2SO_4$ (at natural abundance 0.3665 atoms %^{15}N) was added to increase the sample N content (Shen *et al.*, 1984). When the final combined volume was less than one millilitre the solution was transferred by micropipette to a two millilitre disposable sample cup. The concentrated distillates were then frozen until being analyzed for ^{15}N.

Several steps were taken to prevent cross contamination between samples containing ^{15}N (Hauck, 1982; Buresh *et al.*, 1982; Reeder, 1984; Pruden *et al.*, 1985). Firstly, samples from each plot were prepared on separate days. Secondly, after the collection of distillate containing NH_4^+, five millilitres of ethanol were distilled and then the unit was steamed for two minutes with no water in the water jacket before NO_3^- was determined. Ethanol was again distilled and the still steamed. Distillates from NH_4^+ and NO_3^- determinations were evaporated on separate water baths to reduce possible cross contamination with ^{15}N. Between each day the distillation was steamed for prolonged periods with no water in the water jacket.

2.9.4 Kjeldahl digestion of non ^{15}N-fertilized tree biomass samples

Samples were digested using a modified semi micro Kjeldahl digestion procedure. This was adapted from Bremner and Mulvaney (1982), Buresh *et al.* (1982), Nelson and Sommers (1980), Nicholson (1984), and Thomas (1987, unpub.).

Samples were placed in the oven and dried overnight at approximately 60°C. Duplicate samples (approximately 300 mg) were weighed and the exact weight recorded. For woody tissues, approximately 500 mg samples were used.

One sodium sulphate/selenium catalyst tablet (containing one gram Na_2SO_4 and 0.05 g Se) and four millilitres concentrated sulphuric acid were added to a 25 ml calibrated digest tube containing the weighed sample. The rack of 40 tubes was placed in a cold Tecator aluminium digest block. This was heated to 150°C. Once frothing had ceased after approximately 30 minutes, the temperature was raised to 350°C for one hour. Samples were generally clear at this stage and the temperature was raised to 375°C for three hours. Samples were cooled and diluted to 25 ml. Samples were transferred to well-capped bottles for subsequent analysis.

Nitrogen was determined in aliquots of digest, by steam distillation. Ten millilitre aliquots of digest were neutralized with excess 10 M NaOH. Distilled NH_4^+ was collected in five millilitres of 2% boric acid indicator solution and titrated with standardized 0.025 N sulphuric acid. Steam distillation units used were those constructed by Thomas (1987, unpub.). No correction was made for the efficiency of the steam distillation units (Thomas, 1987, unpub.) because recovery of standard ammonium was usually greater than 98%.

Each digest included blanks, EDTA, glycine, and a standard foliage sample. All samples were analyzed in duplicate (Appendix 2.4b). Where the difference between duplicates exceeded three percent of the mean, the analysis was repeated.

The results of this method did not differ significantly ($P = 0.7822$) from those obtained for some samples using sample combustion by the Dumas method (Appendix 2.4c).

2.9.5 Total nitrogen analysis including NO_3^- of pasture samples

For the digestion of pasture samples the above micro Kjeldahl method was further modified using the salicylic acid/sodium thiosulphate procedure to reduce quantitatively NO_3^- to NH_4^+ (Pruden *et al.*, 1985). Salicylic acid/sulphuric acid mixture was prepared by dissolving 50 g salicylic acid in two litres sulphuric acid. Four millilitres of this solution were added to approximately 200 mg pasture subsamples and left to stand overnight. Using a calibrated scoop approximately 0.5 g sodium thiosulphate pentahydrate was added. Tubes were shaken and gently heated in a cold digest block to 150°C until frothing had ceased. After cooling, one sodium sulphate/selenium tablet was added, the temperature was raised first to 350°C for one hour and then finally to 375°C for three hours. Total N was determined as in Section 2.9.4.

Preliminary investigation showed that 96.5% of NO_3^- added to pine needles could be recovered. To check recovery of NO_3^-, KNO_3 crystals were added to two tubes in each digest. Average recovery was 98% (Appendix 2.4d).

2.10 Soil moisture measurements

2.10.1 Installation of access tubes for neutron moisture meter

A neutron moisture meter was used to monitor weekly changes in soil moisture storage between May 1988 and May 1989. The theory and application of neutron moisture meter studies is discussed by Bell (1976) and Greacen (1981).

Two tubes were installed in one plot of each treatment; two extra tubes were located in the spray-plus-N and one extra in the simulated-grazing-plus-N treatments. Soil samples were taken with a corer designed to obtain relatively undisturbed soil cores of known volume; these samples were used for bulk density and soil moisture determinations. The cores were approximately 96 mm long and 35 mm diameter. The corer consisted of a detachable stainless steel cutting head attached by two recessed grub screws to a chuck which was threaded onto a length of one inch water pipe with a detachable handle.

A raised wooden frame was constructed to protect the core hole opening and surrounding soil surface from disruption and damage. At each location of an access tube the corer was driven with a mallet through the centre of the frame in increments of 96 mm relative to the top of the frame ensuring that the volume of the soil samples was the same. Care was taken not to enlarge the diameter of the core hole while collecting soil samples so as to minimize errors in neutron counts.

After each core had been taken, the depth of the core hole relative to the top of the frame was recorded. The length of the actual core was then calculated and it was this measurement that was used as the length of the core taken. It was not possible to weigh cores in the field so cores were placed in sealed plastic bags and the fresh weight was obtained that night. Intact cores were oven-dried at 105°C for at least 72 hours and re-weighed; bulk density, moisture factor and volumetric water content were calculated.

Access tubes were installed to 1.4-2.3 m depth by first pushing the core hole by hand and then by driving with a large wooden mallet, using a lead cap to protect the top of each tube. Any soil material that fell into the core hole was removed with a hand-driven screw auger. Tubes were left with 100 mm exposed above the soil surface.

This method was used for the installation of eight of the 15 tubes. The other seven tubes were installed using a motorized auger for the surface 60 cm of soil followed by hand auguring. The hole was augured through the access tube with the tube being driven at the same time so that a closely fitting hole was maintained at all times. This method did not allow the determination of bulk density, etc. for these tubes. Tubes were installed between 26 May and 15 September 1988.

In this study a Campbell Pacific Nuclear neutron moisture meter was used with 30 second counts being taken every 10 cm from the soil surface. Shield counts were taken before and immediately after the logging of each tube. Data were processed on a Vax computer using programs supplied by J. Payne (Forest and Wildlands Ecosystem Centre, Forest Research Institute, Christchurch). The stability of the neutron moisture meter was regularly checked by J. Payne using standardized drum conditions.

Field capacity of the soil was determined by flooding a two metre radius around one tube and allowing the profile to drain for 24 hours after neutron moisture meter readings indicated a state of little change in the top 80 - 100 cm. Soil moisture deficits were calculated as the difference between this value and regular weekly neutron moisture readings in the top 10 - 100 cm soil depth.

2.10.2 Calibration of the Campbell Nuclear Pacific neutron moisture meter

Greacen *et al.* (1981) have discussed in detail the methods for calibrating the neutron moisture meter. However, if changes in soil moisture storage are the express purpose of the study then only the slope of the calibration curve of count rate against moisture is important, and for most soils the difference in calibration lines is small (Bell, 1976). The Campbell Nuclear Pacific neutron moisture meter used in this study was provided by Forest and Wildlands Ecosystem Centre, Forest Research Institute, Christchurch, and has been drum-calibrated using two known volumetric water contents, 35 and 100% (R.J. Jackson, Forest and Wildlands Ecosystem Centre, Forest Research Institute, Christchurch, pers. comm.). The water contents obtained using the neutron moisture meter were checked against volumetric water contents and bulk densities obtained during installation of the access tubes (Beets, 1977; Parfitt *et al.*, 1985). Agreement was good (Appendix 2.5).

Chapter Three

Ecosystem productivity

3.1 Introduction

Tree height and root collar were measured every month to monitor their response to treatments. Above and belowground biomass was assessed at the end of the experiment and needle growth assessed on a monthly basis. Growth and dry matter production of pasture in simulated-grazing treatments were assessed during the experiment with successive clippings while in the rank treatments a single sampling took place at the end of the experiment.

3.2 *P. radiata* growth

Repeated measures analysis of variance using pre-treatment height, measured in January 1988 as a covariate for the period August 1988 to May 1989, showed that the probability of significant changes in tree height from one sampling date to another was 0.095 and the interaction of time with pasture competition was 0.095 (Appendix 3.1a). It is possible that these effects were not highly significant because of the short measurement period. However, the trees in the sprayed plots were taller ($P = 0.0002$) than those on the pasture.

This response in tree height to the spray treatments was also illustrated by the analysis of final tree heights (Appendix 3.1b).

Trees started to grow in all treatments in early September and ceased in all treatments, except spray and spray-plus-N, in January (Fig. 3.1). They began to grow again in all treatments in March. Height growth was most rapid in all treatments between September and November despite this being a period of low rainfall (Section 2.2); only 29.9 mm were recorded compared with the long-term average (1965-1990) of 112 mm.

Root collar diameter proved more sensitive to treatment responses. Repeated measures analysis of variance, using pre-treatment root collar diameter^2 measured in January 1988 as a covariate, found significant changes in root collar diameter^2 between sampling dates and a highly significant interaction between time and the level of pasture competition ($P = 0.0003$) (Appendix 3.2a). The effect of removing competition between *P. radiata* and pasture by spraying became apparent by October; root collar diameter growth stopped in all but the sprayed treatments between December and January (Fig. 3.2). By the end of the experiment removing pasture produced a 22% increase in root collar diameter^2 which was significant ($P = 0.0001$) (Appendix 3.2b). There was no response to N.

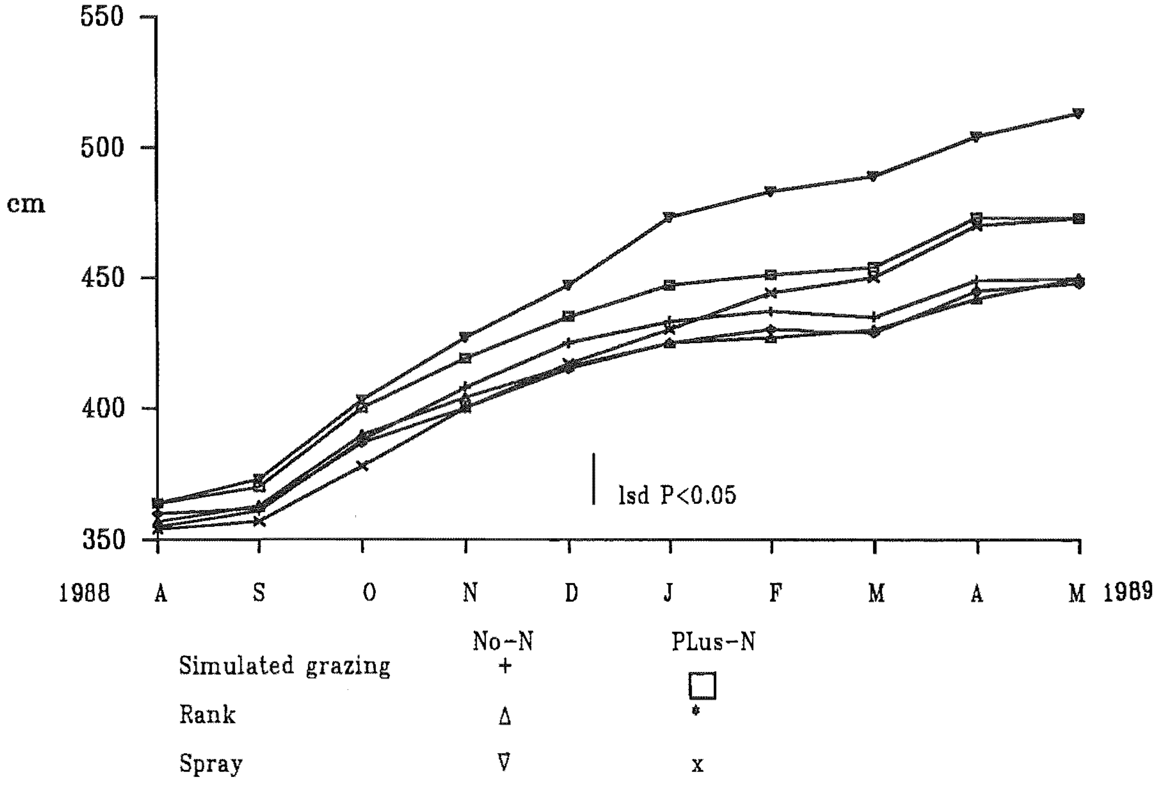


Figure 3.1 **Pattern of tree height growth adjusted for initial height differences using January 1988 measurements, August 1988-May 1989.**

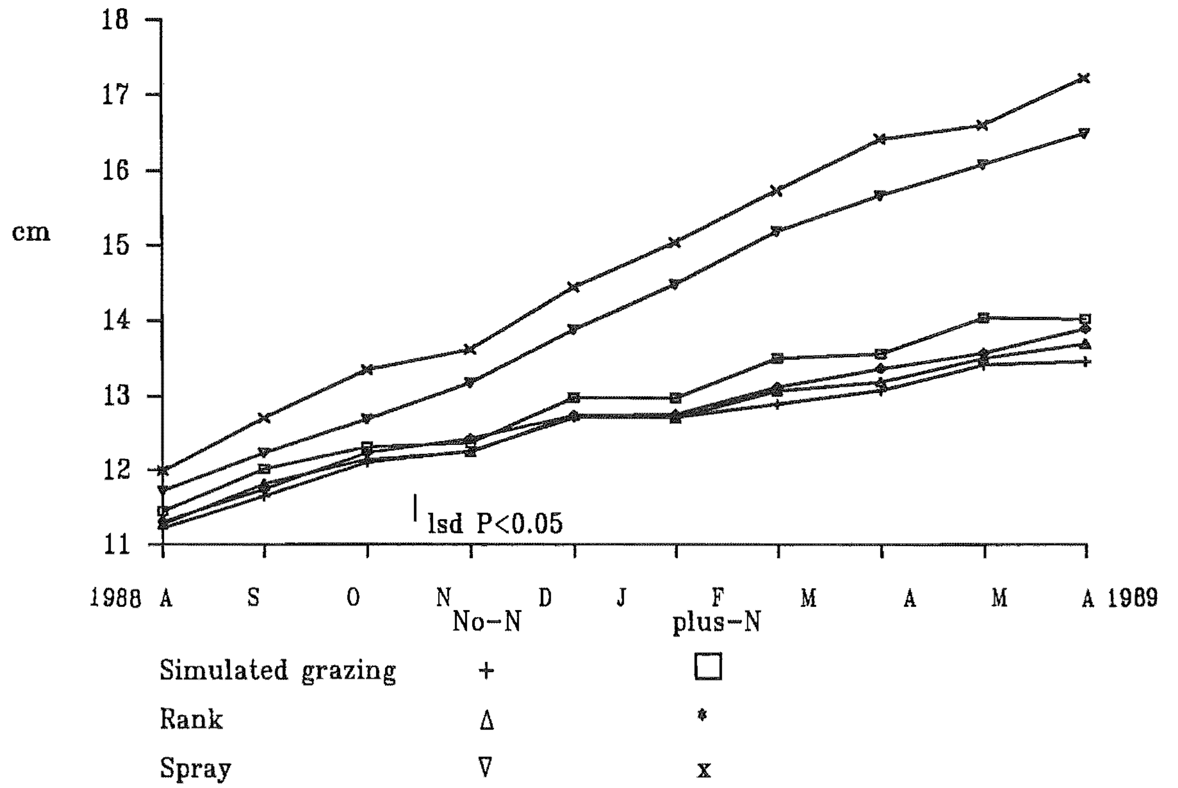


Figure 3.2 **Pattern of root collar diameter growth adjusted for initial diameter differences using January 1988 measurements, August 1988-September 1989.**

3.3 Pasture biomass

3.3.1 Pasture growth in simulated-grazing treatment

Dry matter production in the simulated-grazing treatment was assessed on 11 occasions during the experiment. Repeated measures analysis of variance, using pre-treatment harvest weight as a covariate, showed highly significant changes in the quantity of dry matter removed as a result of seasonal influences (P = 0.0001) (Fig. 3.3). There was a significant response to N fertilizer at P = 0.0069 and P = 0.0245 for dry matter production and pasture production rate, respectively (Appendix 3.3); the interaction was not significant at P = 0.05 level.

Maximum rate of dry matter production occurred between 26 September and 10 October (Fig. 3.4) by which time plus-N plots had received 187 kg N/ha while the no-N plots had still received no N. Dry matter production was strongly affected by the drought and daily production fell to less than 8 kg dry matter/ha between 28 November and 5 January. There was an increase in pasture production rate in late summer to about pre-treatment levels.

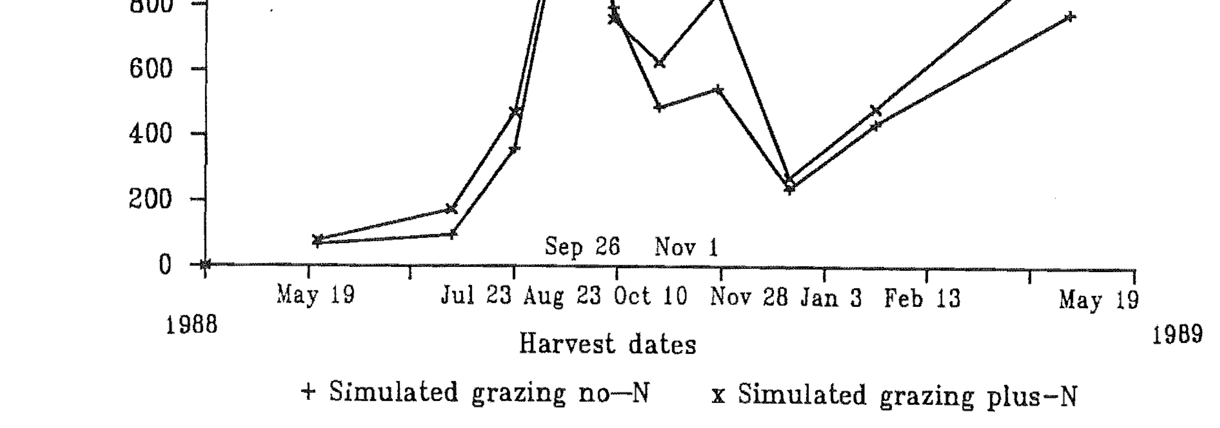


Figure 3.3 Dry matter removed at each harvest of simulated-grazing treatment adjusted for initial harvest differences in March 1988.

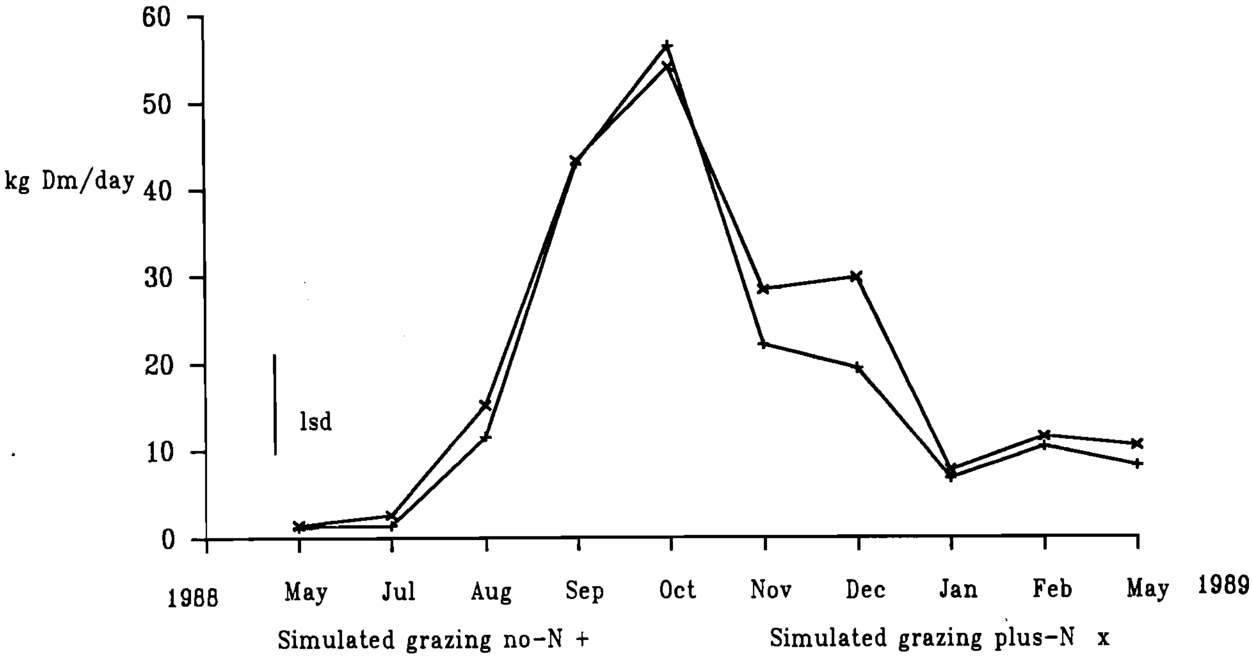


Figure 3.4 Pasture production rate adjusted for pre-treatment differences in production rate per hectare.

The total pasture production in the simulated-grazing treatments was compared to the dry matter production in the rank treatments measured at the end of the experiment (Table 3.1a). There was a highly significant interaction (P = 0.0004) between applied N and level of pasture management (Fig. 3.5, Appendix 3.4a). Adding N at 30 kg/ha month increased total dry matter production by about 20% in the simulated-grazing treatment whereas it led to a 250% increase in the rank treatments.

Table 3.1a Total dry matter removed in simulated-grazing and rank treatments outside the rooting zone of trees, May 1988-May 1989.

Grazing		Rank		
Plus-N	No-N	Plus-N	No-N	S.E.[1]
		kg/ha		
6430	5534	5107	2093	403.8

[1] Standard error.

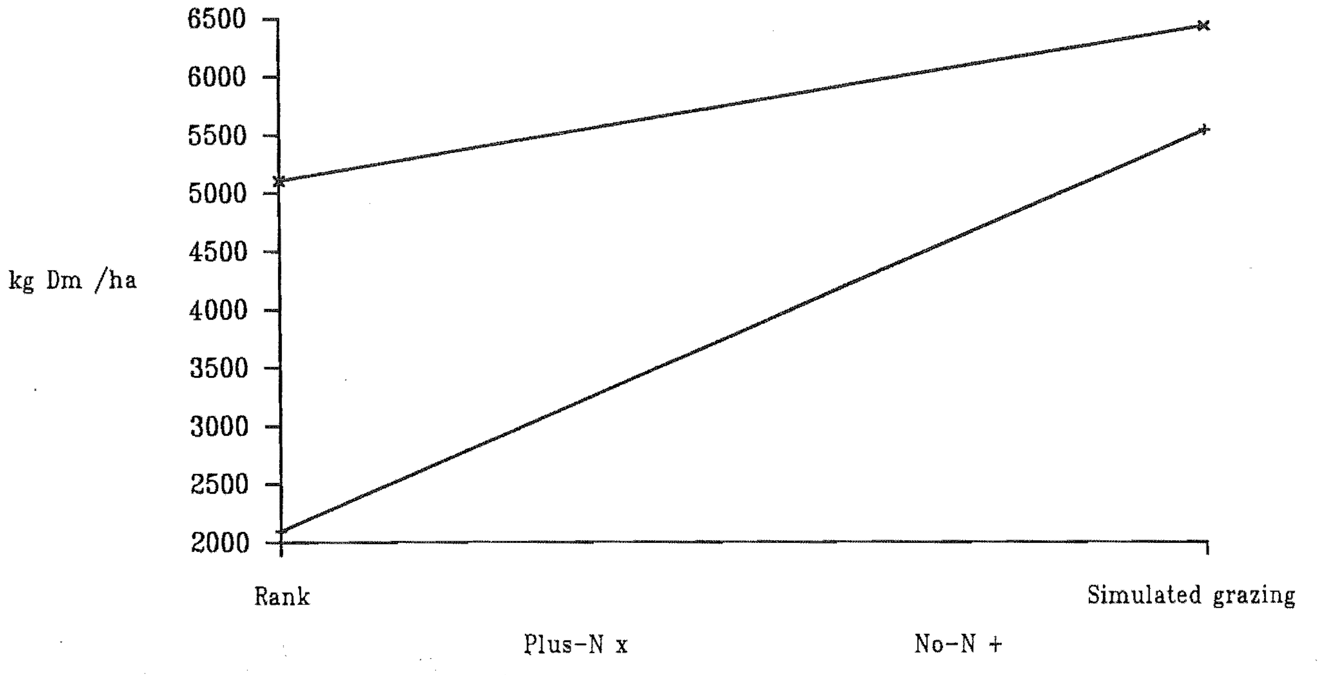


Figure 3.5 Interaction of added nitrogen and level of competing vegetation on aboveground dry matter production.

Total pasture production directly beneath the trees in a 1.9-m-radius area was also assessed between August 1988 and May 1989 as part of the ^{15}N study (Table 3.1b). A comparison of the data for the two locations showed that the production estimates were significantly different (P = 0.0123) and that the average difference between the two locations was 163 g dry matter/m^2 for simulated-grazing-plus-N and rank-no-N and plus-N treatments (Table 3.2).

Table 3.1b Dry matter removed in simulated-grazing and rank treatments inside tree rooting zone, August 1988-May 1989.

Grazing		Rank	
Plus-N	No-N	Plus-N	No-N
	g/m^2		
312	277[1]	266	225

1 Estimate based on ratio between the two sampling positions for the simulated-grazing-plus-N treatment.

Table 3.2 **Comparison of pasture production estimates for two sampling locations.**

0.5 x 0.5 m between trees	1.9-m-radius plots beneath trees
dry matter g/m^2	
430 (173.5[1])	266 (106.9)

[1] Standard deviation (n = 12).

3.3.2 Pasture root biomass

Pasture root biomass was assessed at the end of the experiment and was not estimated for the sprayed treatments although considerable quantities of roots that were considered to be alive still persisted eight months after plots were first sprayed (P. Houston, 1989, unpub.).

Treatments had a significant effect on aboveground dry matter production (Fig 3.5); there were less stubble and roots in the simulated-grazing treatment (P=0.19), (Table 3.3, Appendix 3.4b). Pasture root biomass beneath the 0.5 x 0.5 m plots, at the final harvest, was estimated from the root:shoot ratios obtained from the 1.9-m-radius circular plot beneath the trees (Table 3.4).

Table 3.3 **Belowground pasture biomass (stubble and roots) in the top 20 cm of soil beneath the trees.**

	Grazing		Rank		
Soil depth (cm)	Plus-N	No-N	Plus-N	No-N	S.E.[1]
	dry matter g/1.9-m-radius plot				
0-10	249.2	164.3	373.1	274.8	83.74
10-20	9.4	9.9	8.5	11.5	2.51
0-20	258.7	174.1	381.6	286.3	84.95

[1] Standard error.

Table 3.4 **Estimates of belowground pasture biomass (stubble and roots) in the top 20 cm of soil for 0.5 x 0.5 m plots located outside the rooting zone of trees.**

Grazing		Rank	
Plus-N	No-N	Plus-N	No-N
g/m^2			
107	104	814	313

3.4 *P. radiata* biomass

The aboveground biomass was determined for 26 trees; belowground biomass for 20 of these was also assessed. Differences between treatments were studied by comparing component dry weights, differences in allocation and by examining differences in allometry using the allometric relationship $y = a + bx$.

3.4.1 Aboveground *P. radiata* biomass

P. radiata biomass was examined using analysis of covariance - d^2h was used as the covariate where d is the pre-treatment root collar and h is the pre-treatment height (measured in January 1988). This was the best of two covariates tested (Appendix 3.5). Adjusted treatment means for various components are shown in Table 3.5. There was no significant interaction of applied N and level of competing vegetation (Appendix 3.6a).

Significantly different regressions were found for the biomass of two-year-old needles and coarse roots larger than one millimetre diameter using d^2h as a covariate (Appendix 3.6a). The relationship between two-year-old needle biomass and d^2h illustrated in Figure 3.6a shows that the rank-plus-N treatment behaved differently from the others: as two-year-old needle biomass decreased tree size increased (Appendix 3.6b). This may suggest that large trees in this treatment were under more moisture stress than in other treatments.

In contrast with other treatments coarse root biomass in the rank-no-N treatment did not increase (Fig. 3.6b) and is probably attributable to the stress that large trees in this treatment were undergoing.

All tree components except older needles, older stem wood and fine roots, show significant responses ($P < 0.05$) to the spraying treatment (Appendix 3.6a). There were no statistically significant differences between N treatments and between rank and simulated-grazing treatments for any biomass variable (Appendix 3.6a). Removing pasture competition by spraying increased whole tree biomass by 55%. This response was evenly allocated between above and belowground biomass pools. The spraying treatment doubled current needle biomass which in turn lead to an 88% increase in aboveground net primary production. Although no direct measurements were made of efficiency of photosynthesis it may be estimated that in the sprayed treatments there was a 12% increase in the quantity of dry matter produced aboveground per unit of needle weight.

Table 3.5 **Oven-dry weights of *P. radiata* biomass components adjusted for initial tree size effects using pre-treatment d^2h measured in January 1988.**

	Grazing		Rank		Spray		
Tree components	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			g/tree				
Foliage							
Current	5474	4846	6379	4102	11289	10591	1019.1
1-year-old	3665	3463	3403	3626	3994	4120	479.7
2-year-old[2]	1335	563	884	641	767	949	329.0
Total	10117	9065	10616	8321	16213	15795	1380.4
Branches							
Current	1823	1536	2688	1705	3514	3909	553.3
Older	5689	7312	6845	7191	9562	10553	1035.7
Stem wood							
Current	4717	3510	3493	3775	6528	6178	594.7
Older	4481	3983	4066	3980	4568	3999	312.2
Buds	199	118	223	173	544	548	117.3
Bark							
Current	65	54	61	65	97	169	15.7
Older	1202	1316	1119	1201	1736	2287	187.1
Total aboveground	28288	26859	29109	26410	42764	43440	2964.1
Roots							
Fine roots[3]	303	244	189	245	172	233	56.9
Coarse roots[2]	3262	2320	4068	2568	4819	4778	829.9
Stump	3953	4214	4464	4535	5719	4758	289.9
Total belowground	5134	5730	6520	5436	9012	8771	661.5
Total tree	33423	32588	35629	31845	51775	52210	3489.5

1 Standard error.
2 Non-parallel slopes, $P < 0.05$, unadjusted means presented.
3 Roots < 1 mm diameter.

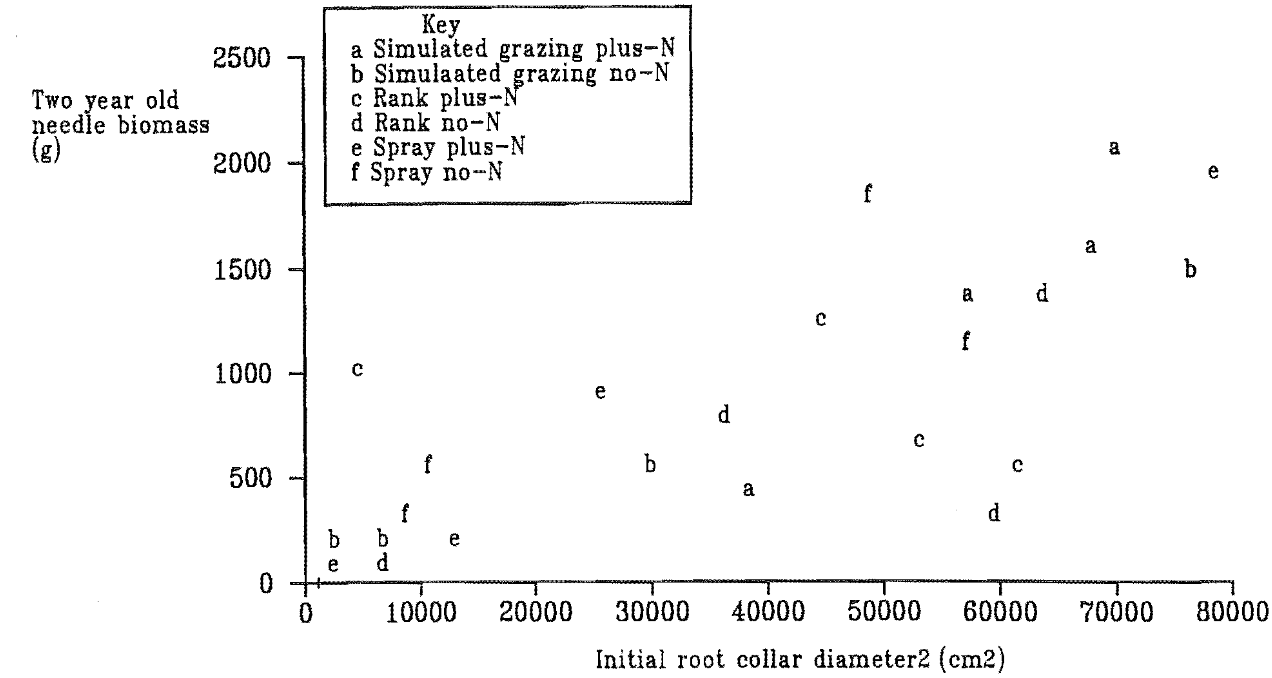


Figure 3.6a Interaction between treatment and two-year-old needle biomass.

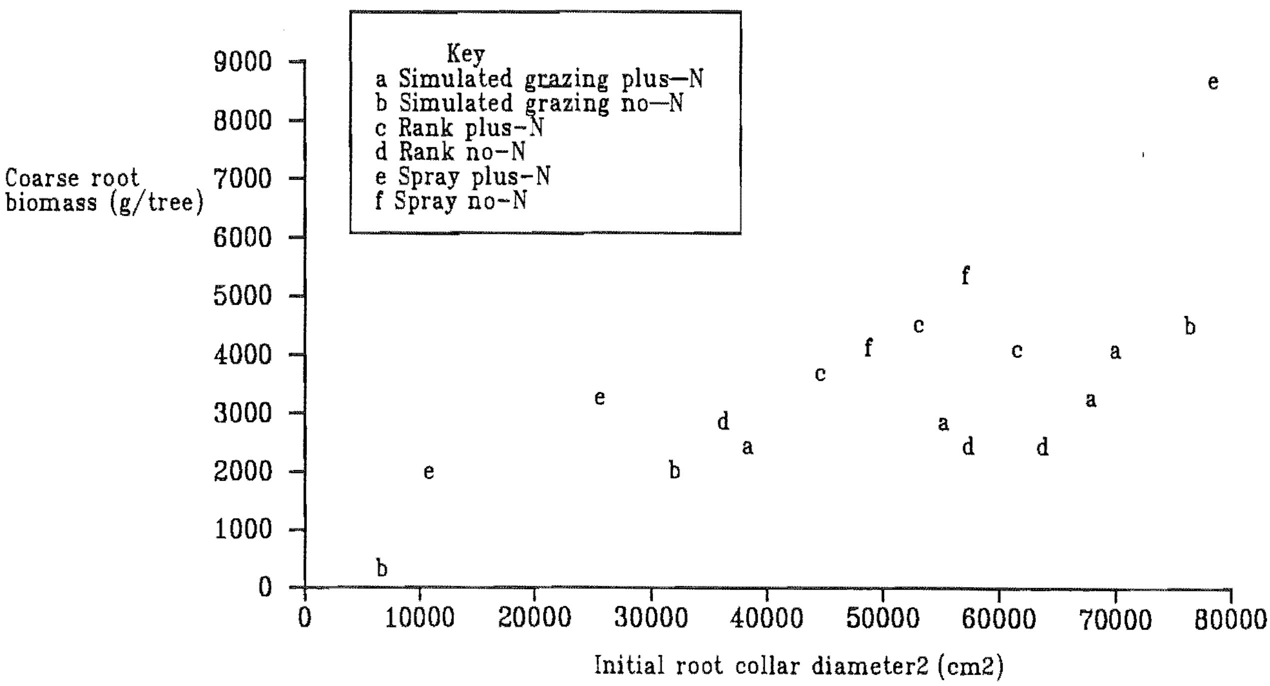


Figure 3.6b Interaction between treatment and coarse root biomass.

3.4.2 Distribution of biomass within the crown of *P. radiata*

The relative distribution of biomass in the crown of *P. radiata* before and after treatment is shown in Table 3.6 and indicates very little difference between treatments.

For both branches:crown and stem:branches ratios, interaction of added N and level of competing vegetation was not significant ($P > 0.05$) (Appendix 3.7). However, there was a significant increase in allocation of biomass to crown compared to stem in treatments without pasture compared with simulated-grazing and rank treatments (Table 3.7, Appendix 3.7).

Analysis of crown distribution patterns using the allometric equations:

$$\textit{Ln stem weight} = a_o + a_i \textit{ (Ln crown weight)},$$
$$\textit{Ln stem weight} = a_o + a_i \textit{ (Ln branch weight)}$$

showed that there were no significant differences between treatments ($P = 0.6218$ and $P = 0.6689$ respectively).

The pooled equations suggested that crown and branch growth were proportionally greater than stem growth (Tables 3.8a and 3.8b).

Table 3.6 Distribution of aboveground biomass in *P. radiata* at the start of the trial and as influenced by treatment at the final harvest.

	Grazing		Rank		Spray		
	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	Initial
			%				
Foliage	36	36	36	34	38	37	36
Branches	27	31	33	31	31	34	29
Stem	37	33	31	35	31	29	35

Table 3.7 The effect of treatment on ratios of stem:crown and stem:branches.

	Grazing		Rank		Spray		
	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
Stem[2]:crown[3]	0.566	0.567	0.441	0.516	0.425	0.396	0.4474
Stem:branches	1.268	1.542	1.084	1.1302	0.992	0.864	0.1938

1 Standard error.
2 Wood plus bark.
3 Foliage plus branches.

Table 3.8a **Regression equations for the allometric relationships of crown weight on stem weight as influenced by competition and nitrogen application.**

Treatment	a_o	S.E.[1]	a_i	S.E.	r^2	P[2]	n
Grazing							
Plus-N	-0.988	3.004	1.018	0.296	0.7833	0.0751	4
No-N	-2.867	0.193	1.214	0.021	0.9991	0.0003	4
Rank							
Plus-N	-3.720	0.628	1.292	0.064	0.9926	0.0025	4
No-N	-3.360	0.980	1.269	0.101	0.9810	0.0063	4
Spray							
Plus-N	-1.171	0.296	1.033	0.030	0.9975	0.0008	4
No-N	-2.993	1.841	1.219	0.181	0.9366	0.0213	4
Overall	**-0.073**	**0.485**	**0.931**	**0.049**	**0.9385**	**0.0001**	**24**

1 Standard error of parameter.
2 Probability of regression equation.

Table 3.8b **Regression equations for the allometric relationships of branch weight on stem weight as influenced by competition and nitrogen application.**

Treatment	a_o	S.E.[1]	a_i	S.E.	r^2	P[2]	n
Grazing							
Plus-N	5.349	3.711	0.418	0.388	0.0518	0.3935	4
No-N	-3.935	0.385	1.425	0.045	0.9969	0.0010	4
Rank							
Plus-N	-2.795	0.771	1.308	0.086	0.9871	0.0043	4
No-N	-1.660	1.132	1.173	0.125	0.9662	0.0113	4
Spray							
Plus-N	-0.286	0.871	1.034	0.097	0.9740	0.0087	4
No-N	3.519	3.799	0.038	0.411	0.3183	0.2614	4
Overall	**2.009**	**0.435**	**0.784**	**0.048**	**0.9187**	**0.0001**	**24**

1 Standard error of parameter.
2 Probability of regression equation.

3.4.3 *P. radiata* root biomass

Total belowground biomass showed a significant response to the spraying treatment alone with no interaction with applied N (Appendix 3.6a). Removing competition significantly increased ($P < 0.001$)[1] belowground *P. radiata* root biomass by 56%.

The root:shoot ratio was not influenced by the treatments (Table 3.9, Appendix 3.9).

Table 3.9 Root:shoot ratio of *P. radiata* as influenced by treatment.

	Grazing		Rank		Spray		
	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E[1].
Root:shoot ratio	0.203	0.251	0.232	0.219	0.195	0.205	0.3803

1 Standard error.

Ledig *et al.* (1970) recommended using allometric relationships between shoot weight and root weight $Ln\ (shoot\ weight) = a_o + a_i\ (Ln\ root\ weight)$ rather than root:shoot ratios, because this method removes the potential effect of varying tree size. A statistically significant relationship was only found for the rank-no-N treatment (Table 3.10). The slope (a_i) was greater than one showing that shoot growth has a proportionally greater increase than root growth for this treatment. Slopes of the regression equations in Table 3.10 show that slopes (a_i) for rank-plus-N and spray-plus-N are less than one. For these treatments root growth has a proportionately greater increase than the shoot. However, these regressions are not significant. Due to low sampling it was not possible to calculate the relationship for the spray-no-N treatment.

There is little evidence to suggest that experimental treatments altered the allocation of photosynthate between roots and shoots because the regression coefficients are similar ($P > 0.05$). For the pooled regression the slope is greater than one suggesting that, overall, the relative growth of the shoot was greater than the root during the experiment.

There were no significant differences between treatments in the quantity of roots less than one millimetre diameter (Appendix 3.6a) and the pooled mean was 92.3 kg/ha in the surface 20 cm of soil.

1 The analysis refers to a full four replications per treatment and included one estimated value from each of the simulated-grazing-no-N, rank-plus-N, rank-no-N and spray-plus-N treatments and two from spray-no-N treatment (Appendix 3.8). These should not be treated as normal samples and the degrees of freedom should be reduced by subtracting six degrees of freedom; this adjustment lowers the F value from 34.3 to 22.19, P is therefore still less than 0.01.

Table 3.10 Regression equations for the allometric relationships of root on shoot, as influenced by pasture and nitrogen application: *Ln shoot weight* = $a_o + a_i$ *Ln root weight.*

Treatment	a_o	S.E.[1]	a_i	S.E.	r^2	P[2]	n
Grazing							
Plus-N	1.366	2.921	1.026	0.324	0.7499	0.0872	4
No-N	-0.824	1.185	1.264	0.139	0.9759	0.0700	3
Rank							
Plus-N	3.751	4.654	0.749	0.511	0.3645	0.3813	3
No-N	-1.208	0.231	1.306	0.026	0.9992	0.0127	3
Spray							
Plus-N	4.703	0.512	0.663	0.056	0.9856	0.0540	3
No-N[3]							2
Overall	**0.569**	**0.723**	**1.108**	**0.081**	**0.917**	**0.0010**	**18**

1 Standard error of parameter.
2 Probability of regression equation.
3 Not done.

3.4.4 Distribution of pine fine roots in relation to pasture roots in the top 20 cm of soil

There were no significant treatment effects on the vertical distribution of pasture roots and stubble. Nor were there any significant differences in the quantity of pasture root and stubble biomass between the rank and the simulated-grazing treatment. Ninety-six percent of pasture roots and stubble were in the top 10 cm of soil in both simulated-grazing and rank treatments (Section 3.3.2).

While the total amounts of pine fine roots do not differ with treatment (Table 3.5, Appendices 3.6a, 3.10a), the rank and simulated-grazing treatments have significantly higher ($P = 0.034$) proportions of their pine fine root biomass in the top 10 cm of soil than the sprayed treatments (Table 3.11, Appendix 3.10b). Spray treatments have proportionally more fine roots in the 10-20 cm horizon.

Table 3.11 Percent of total *P. radiata* fine roots less than one millimetre diameter in the 0-10 and 10-20 cm soil depths.

	Grazing		Rank		Spray		
Soil depth (cm)	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			%				
0-10	76.0	82.0	70.0	74.0	61.0	66.0	6.3
10-20	24.0	18.0	30.0	26.0	39.0	34.0	-

1 Standard error.

This pattern of vertical distribution of pine fine roots agrees with some of the observations of P. Houston (1989, unpub.) study of pine fine root distribution in the rank-no-N and spray-no-N treatments. In Houston's study there was no treatment effect but in the spring sampling there was 2.5 times more fine roots in the top 10 cm of soil than in the 10-20 cm depth. This difference had disappeared by the summer sampling.

There were no significant differences ($P < 0.05$) in the ratio of pine fine root weight to pasture root weight in the top 20 cm of soil (Table 3.12, Appendix 3.11).

Table 3.12 Ratio of pasture root and stubble:pine fine root weight in top 20 cm of soil in the 11.341 m^2 plots.

Grazing		Rank		
Plus-N	No-N	Plus-N	No-N	S.E.[1]
	g/g			
14.7	19.4	66.2	22.0	23.6

1 Standard error.

3.5 Needle growth

Needle weight data from October 1988 to May 1989 were logarithmically transformed and statistically analyzed using repeated measures analysis of variance. Untransformed means are presented graphically. There were no significant interactions between added N and the level of competing vegetation (Appendix 3.12a). One-year-old needles in the upper (Fig. 3.7) and lower crown showed no significant changes in weight from one sampling date to another or as a result of treatments (Appendices 3.12a and 3.12b). For current needles in the lower (Fig. 3.8), upper (Fig. 3.9) and uppermost crown positions, there were highly significant increases in needle weight between each sampling date for all treatments ($P = 0.0001$).

In both positions needle weight increases rapidly between November 1988 and February 1989, thereafter current needle weight changes very little, especially in the lower crown. Current needles in the upper and uppermost crown show significant interactions between sampling date and level of pasture competition ($P = 0.0060$ and 0.0015 respectively).

By December it is apparent that in the uppermost crown, current needles are heavier in the sprayed treatment and lightest in the rank treatment. Current needles in the simulated-grazing treatment are of intermediate weight and this pattern persists until May; and the difference between the rank and sprayed treatments continues to increase.

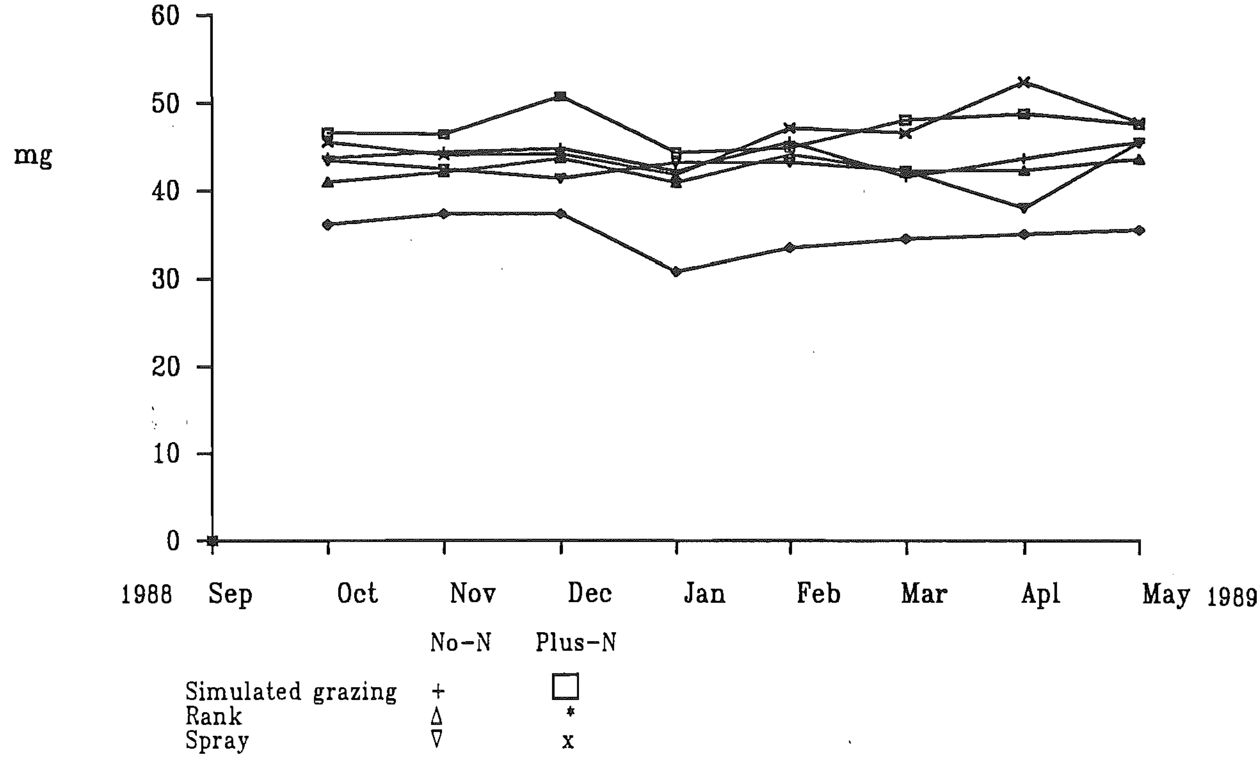


Figure 3.7 Seasonal course of weight per needle for one-year-old needles in the upper crown.

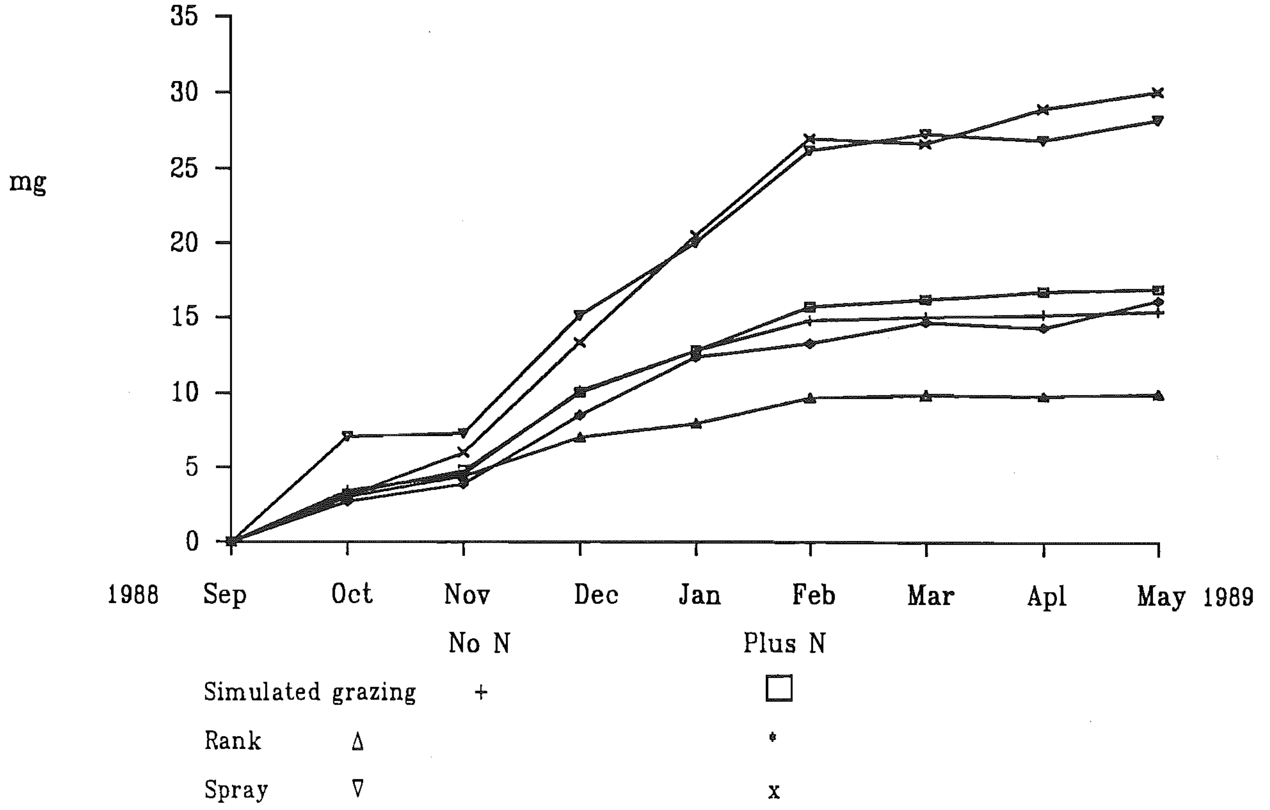


Figure 3.8 Seasonal course of weight per needle of current needles in the lower crown.

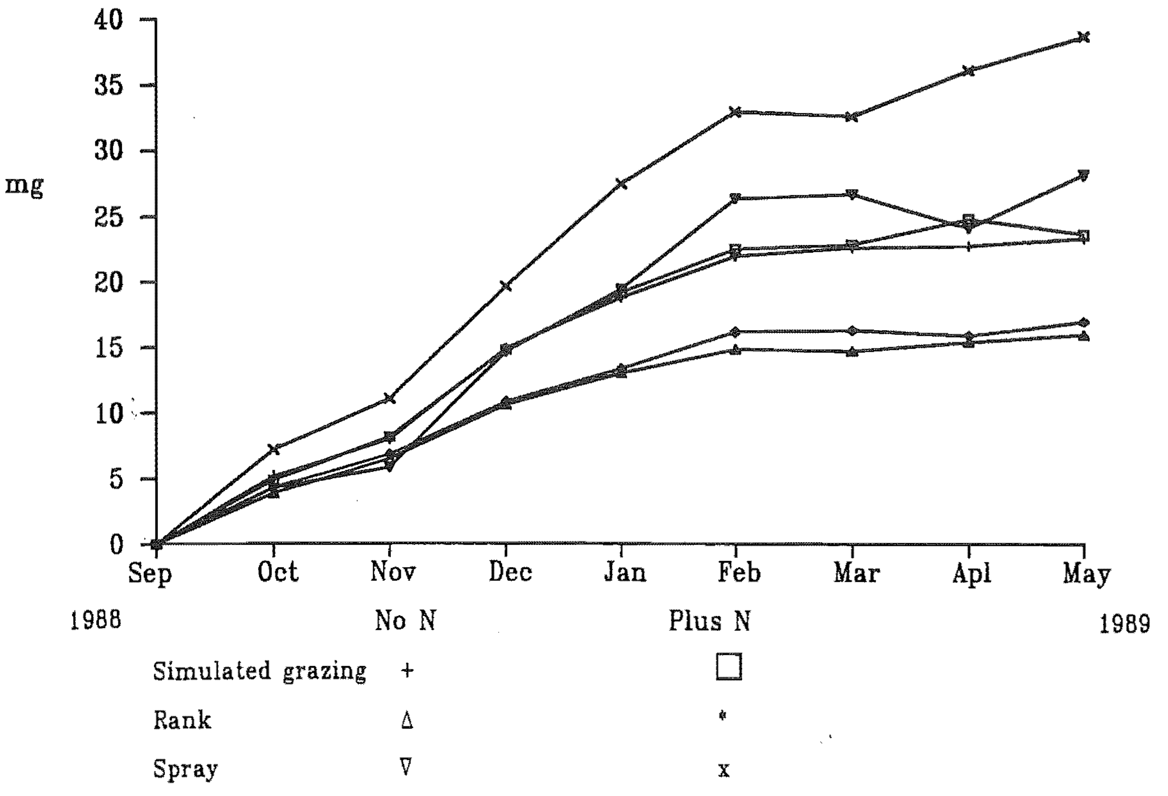


Figure 3.9 **Seasonal course of weight per needle of current needles in the upper crown.**

Table 3.13 **Estimated number of needles per tree at final harvest.**

	Grazing		Rank		Spray		
	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			number of needles x 1000				
Actual	715	381	620	468	663	545	147
Adjusted	569	463	611	459	675	618	105

1 Standard error.

Estimates of needle number by crown position were calculated by dividing needle mass of each crown position by the weight per needle at the May 1989 needle collection (Table 3.13). Due to differences in initial tree size covariance analysis was used. There were no treatment effects on total tree needle number (Appendix 3.13). This analysis therefore suggests that the time course of needle weight is a reasonable indication of total foliage biomass development.

3.6 Combined tree and pasture production

Aboveground net primary production for trees was calculated from the sum of current needles, increment in wood (Table 3.5), bark and branches (Appendices 3.14b and 3.14c) and is shown in Table 3.14. Aboveground pasture production was weighted by area for the two production estimates (Tables 3.1a and 3.1b) and is also shown in Table 3.14.

Aboveground production of trees was substantially increased when competition between pasture and trees was eliminated by spraying. Addition of split application of N did not have the same effect. Pasture production was increased by the addition of N and also by the simulated-grazing treatment but overall aboveground system production (tree plus pasture) was fairly similar between all treatments (Table 3.14), with sprayed treatments showing only a 5.6% increase over the plus-pasture treatments.

Table 3.14 Aboveground production for pasture and trees, August 1988-May 1989.

	Grazing		Rank		Spray	
	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N
			T/ha			
Total tree aboveground production[1]	4.66	4.85	5.42	4.65	8.87	9.16
Pasture[2] aboveground production	4.39	3.91	3.99	2.25	0	0
Total current production (trees + grass)	9.05	8.76	9.41	6.90	8.87	9.16

1 Aboveground net primary production = $\sum$ current needles, increment in wood, bark and branches.
2 Area weighted adjusted mean.

3.7 Summary

- Tree height and root collar diameter growth were increased by the spraying treatment with root collar diameter showing a 22% increase.

- Pasture production was increased by the addition of N and the simulated-grazing treatments.

- Pasture root biomass directly beneath trees was not affected by either split application of N or the simulated-grazing treatment.

- Removing pasture competition increased aboveground *P. radiata* biomass by 55% and this was mainly due to an increase in needle and branch biomass.

- Total system aboveground production (trees plus pasture) was apparently not affected by treatment.

Chapter Four

^{15}N dynamics

4.1 Introduction

In this study of the competition for N in a simulated agroforestry ecosystem, ^{15}N dynamics were examined to identify the mechanisms involved.

The dynamics of ^{15}N in the soil and plants were quantified by tracing ^{15}N in total soil N and KCl-extractable mineral N pools, along with ^{15}N uptake into the pasture and foliage of the trees. These measurements elucidated information on the competition for N between trees and pasture. In the simulated-grazing treatment, application of $^{15}NO_3^-$ and $^{15}NH_4^+$ was used to examine the uptake by trees and pasture for different forms of plant-available N, and to follow transformation (immobilization, mineralization, nitrification) patterns.

4.2 Soil ^{15}N dynamics

4.2.1 Proportion of nitrogen derived from ^{15}N-labelled fertilizer in soil

The proportion of N derived from ^{15}N-labelled fertilizer was calculated using Formula 4.1.

Formula 4.1 $$\%Ndff = \frac{c - b}{a - b} \times \frac{100}{1}$$

a: atom $\%^{15}N$ in the labelled fertilizer
b: atom $\%^{15}N$ in the unfertilized component
c: atom $\%^{15}N$ in the fertilized component

The proportion of total soil N derived from ^{15}N-labelled fertilizer (%Ndff) was assessed in the 0-10 cm soil depth collected at 14, 154, and 249 days after application (Table 4.1).

There were no significant time and time x treatment interactions for %Ndff in total soil N ($P < 0.05$) (Table 4.1, Appendix 4.1a). However, on average, %Ndff was higher in the sprayed plots than in the plots with pasture ($P = 0.04$) and there were no other significant differences (Appendix 4.1a). By the end of the experiment differences were not significant (Appendix 4.1b).

It was expected that %Ndff in total soil N would progressively decline because of plant uptake and the continued addition of non-labelled N to the plus-N treatments. Data suggested a decline except in the $^{15}NO_3$-treated simulated-grazing plots, but the changes were not significant (Table 4.1). The sprayed treatment showed a 30% decline in %Ndff during the 249-day period and this is thought to be due to plant uptake, dilution by added N, and the possible loss of ^{15}N-labelled-N by denitrification.

Table 4.1 Dynamics of the %Ndff in total soil nitrogen in the 0-10 cm soil depth, September 1988-May 1989.

	Grazing		Rank	Spray	
Day	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
		%			
14	0.326	0.431	0.481	0.657	
154	0.305	0.395	0.478	0.477	
249	0.370	0.373	0.437	0.462	
Mean	0.334	0.400	0.465	0.517	0.0447

1 Standard error.

4.2.2 Soil retention of ^{15}N

Recovery of ^{15}N in total soil N was calculated as the product of total N, %Ndff, bulk density and plot volume (Formula 4.2).

Formula 4.2
$$\%^{15}N \text{ recovery} = \frac{\pi r^2 h \times bd \times \%N \times 100 \quad \dfrac{(c-b)}{(a-b)}}{g\ N\ applied}$$

Where $\pi r^2 h$ is the volume to sampled depth; bd is bulk density determined in Section 2.6.3 for each soil depth; a, b and c are as in Formula 4.1; g N applied refers to g of N applied at time of ^{15}N application.

There were no significant time or treatment interactions ($P < 0.05$) for ^{15}N recovery in the soil (Table 4.2, Appendices 4.1a and 4.1b).

For all treatments, except sprayed, there was very little change in the recovery of ^{15}N in total soil N. This suggests that, in those treatments where ^{15}N recovery did not vary greatly, retention of ^{15}N in soil may have been at equilibrium conditions brought about by inputs of ^{15}N to the soil N pool from the death of pine and pasture roots during the period of drought (October to February). The low recovery of ^{15}N in the $^{15}NO_3^-$-treated simulated-grazing plots was due to the high recoveries of ^{15}N removed in clipped pasture.

Table 4.2 Dynamics of total ^{15}N recovery in 0-10 cm soil depth, September 1988-May 1989.

	Grazing		Rank	Spray	
Day	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NO_3^-$	S.E.[1]
		%			
14	35.08	38.06	42.97	66.69	
154	34.40	39.85	43.75	48.82	
249	40.82	35.64	40.53	37.98	
Mean	36.77	37.85	42.42	51.16	7.415

1 Standard error.

4.2.3 Proportion of nitrogen derived from ^{15}N-labelled fertilizer in KCl-extractable mineral nitrogen in soil

Samples for the first collection were bulked by treatment; hence no statistical tests of %Ndff in KCl-extractable mineral N could be made. However, the error mean square from later sampling dates gave an idea of the variability within treatments (Appendix 4.2a) and some differences were very large.

Fourteen days after application, ^{15}N-labelled fertilizer constituted 50 and 65% of the mineral N pools in the $^{15}NO_3^-$-treated simulated-grazing and sprayed treatments respectively, but only 30-35% in the other two treatments.

In all treatments $^{15}NH_4^+$ had been rapidly transformed to $^{15}NO_3^-$, especially in the sprayed treatment where 16% of the soil NO_3^- pool was from the ^{15}N-labelled fertilizer addition. In the $^{15}NO_3^-$-treated simulated-grazing treatment, three percent of the soil NH_4^+ pool was ^{15}N-labelled.

The grazing-plus-N plots treated with $^{15}NO_3^-$ had received 187.5 kg N/ha, of which 108 kg/ha was NO_3^--N. As would be expected, $^{15}NO_3^-$ contributed greatly to the soil pool of NO_3^- in the $^{15}NO_3^-$-treated plots (Table 4.3). In contrast, the contribution of $^{15}NH_4^+$ to the soil pool of NH_4^+ was smaller and more of the $^{15}NH_4^+$ has been transformed to $^{15}NO_3^-$ than vice versa. In these soils it is apparent that $^{15}NO_3^-$ remained available for plant uptake longer than $^{15}NH_4^+$, given the conditions that existed at the time of ^{15}N application. Probably the $^{15}NH_4^+$ was immobilized or underwent transformation and hence was less available to plants. However, the levels of %Ndff were considerably higher in the sprayed plots indicating that there must have been very rapid utilization of the fertilizer by pasture. For all treatments there was a considerable decline in levels of %Ndff by Day 154 and no further changes in any treatment were apparent by Day 249 (Table 4.3, Appendix 4.2a).

Table 4.3 **%Ndff in KCl-extractable mineral nitrogen in the 0-10 cm soil depth, September 1988-May 1989.**

		Grazing		Rank	Spray
Day		$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$
			%		
14	$^{15}NH_4^+$	2.8	25.4	29.9	43.9
	$^{15}NO_3^-$	47.7	4.1	4.7	15.7
154	$^{15}NH_4^+$	1.2	1.8	3.1	3.0
	$^{15}NO_3^-$	3.4	1.6	2.5	3.9
249	$^{15}NH_4^+$	1.0	2.0	2.7	2.7
	$^{15}NO_3^-$	4.1	3.9	2.9	2.3

4.2.4 Total mineral nitrogen pools in the 0-10 cm soil depth

Total pools of KCl-extractable mineral N (NH_4^+ + NO_3^-) were estimated on three occasions, with variability within treatments being assessed on the last two of these. Total pools of soil mineral N were three times as large in the sprayed treatment as in other treatments 14 days after ^{15}N application (Table 4.4).

Prior to the first sampling all treatments had received 187.5 kg N/ha; 107.7 kg of this was NO_3^- (Appendix 4.2b). However, quantities of NO_3^- in all treatments except the sprayed were less than six percent of total N applied to that time. With the removal of vegetation, soil NO_3^- increased to a level of 22% of total applied N and total mineral-N in the soil was equivalent to 38% of the applied N. These low soil pools (Table 4.4) partly reflected the combined demand for N early in spring when tree and pasture growth was rapid (Figures 3.1 and 3.4).

There were no significant treatment effects for total mineral N ($P < 0.05$) (Appendices 4.2b and 4.3a). However, in all treatments there was an accumulation of mineral N in the top 10 cm of soil from September onwards (Table 4.4). This accumulation was the result of the monthly N fertilizer additions, increased mineralization and/or a reduction in plant uptake and immobilization.

4.2.5 Recovery of ^{15}N in KCl-extractable mineral nitrogen in the soil

Samples for the first collection were bulked by treatment; hence no statistical tests of percent ^{15}N recovery in KCl-extractable mineral N could be made. However, recovery of ^{15}N-labelled fertilizer was greatest in the sprayed treatment and, on average, more than four times as much ^{15}N was recovered in plant-available forms 14 days after application of ^{15}N-labelled fertilizer (Table 4.5, Fig. 4.1).

Table 4.4 **Quantities of mineral nitrogen (NH_4^+ + NO_3^-) in the top 10 cm of soil as influenced by treatment and sampling date.**

Day		Grazing	Rank	Spray
			kg/ha	
14	NH_4^+	13.5	12.7	29.3
	NO_3^-	11.5	5.9	41.0
	Total	**25.0**	**18.6**	**70.3**
154	NH_4^+	92.0	49.9	77.9
	NO_3^-	77.8	62.0	139.8
	Total	**169.8**	**111.9**	**217.7**
249	NH_4^+	77.6	48.1	69.6
	NO_3^-	87.0	81.1	99.9
	Total	**164.6**	**129.2**	**169.5**

Table 4.5 **Percent ^{15}N recovery in KCl-extractable soil mineral nitrogen (NH_4^+ + NO_3^-) in the 0-10 cm soil depth as influenced by treatment and sampling date.**

		Grazing		Rank	Spray
Day		$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$
			%		
14	NH_4^+	1.1	11.9	12.6	42.9
	NO_3^-	17.0	1.4	0.9	21.3
	Total	**18.1**	**13.3**	**13.5**	**64.2**
154	NH_4^+	3.5	5.5	6.2	7.6
	NO_3^-	10.0	4.3	5.2	18.0
	Total	**13.5**	**9.8**	**11.4**	**25.6**
249	NH_4^+	3.9	4.8	5.1	6.4
	NO_3^-	17.9	9.0	7.9	7.7
	Total	**21.8**	**13.8**	**13.0**	**14.1**

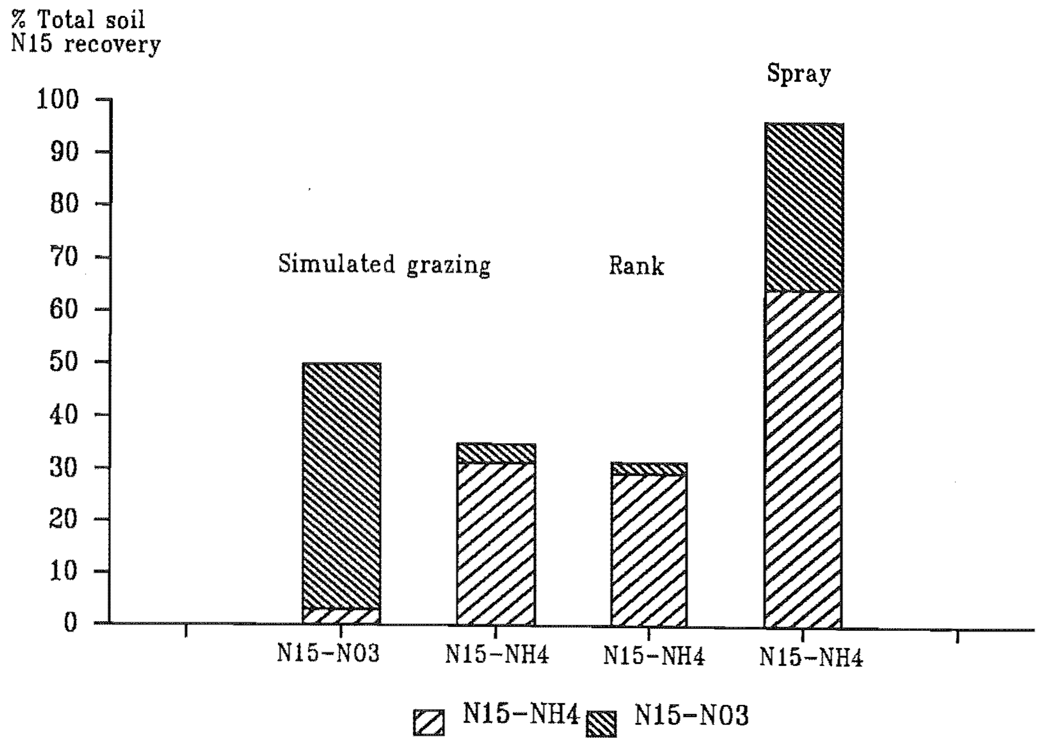


Figure 4.1 **Percentage of total soil ^{15}N recovered as $^{15}NH_4^+$ and $^{15}NO_3^-$ in 1 M KCl extracts in the 0-10 cm soil depth 14 days after application.**

Transformation of applied ^{15}N was rapid and 14 days after application of $^{15}NH_4^+$ to the simulated-grazing and rank treatments, 3.7 and 6.0% of recovered ^{15}N was in the $^{15}NO_3^-$ form (Table 4.5). One third of the $^{15}NH_4^+$ had been nitrified in the sprayed treatment by this time.

By 154 days the recovery of ^{15}N in the sprayed treatment had dropped by 60% and there were no longer any changes or treatment effects that were statistically significant (Appendix 4.2a).

This quantity of ^{15}N recovered as mineral N declined with time from 64 to 14% in the sprayed treatment but remained at about 13 to 20% in the other treatments.

It is interesting to note that there were only small reductions in the $^{15}NO_3^-$ levels in the sprayed and $^{15}NO_3^-$-treated simulated-grazing treatments between 14 and 249 days, and in the other two treatments nitrification continued.

At the end of the experiment there were no significant differences in ^{15}N recovery in NH_4^+-N, NO_3^--N or total mineral N between treatments ($P < 0.05$) (Appendix 4.3b). Less ^{15}N was recovered in the NH_4^+-N fraction than in NO_3^--N and by May (249 days after ^{15}N application) in the rank and simulated-grazing $^{15}NH_4^+$-treated treatments, 61 and 65%, respectively, of the ^{15}N was found as $^{15}NO_3^-$.

4.3 Uptake of ^{15}N in simulated-grazing treatment

The recovery of ^{15}N-labelled N fertilizer in successive harvests of pasture in the simulated-grazing treatment enabled the difference in recovery between applied $^{15}NH_4^+$ and $^{15}NO_3^-$ to be compared. Plots were clipped and sampled at 14, 28, 50, 77, 113, 154, and 249 days after ^{15}N application.

4.3.1 Proportion of nitrogen derived from ^{15}N-labelled fertilizer in pasture samples

There were significant changes in %Ndff from one sampling date to another but there was no significant time x treatment interaction (Fig. 4.2, Appendix 4.4). The decline in %Ndff was due to plant uptake and removal in clippings, as well as immobilization of ^{15}N, especially $^{15}NH_4^+$. Later additions of unlabelled N would also have diluted the ^{15}N in the available N pool.

There are two possible reasons why the %Ndff in the NH_4^+- and NO_3^--treated simulated-grazing treatments became similar after the December sampling: there was a smaller pool of $^{15}NO_3^-$ due to plant uptake; or immobilized $^{15}NH_4^+$ was being mineralized after rainfall events. At the February soil sampling (154 days after ^{15}N-labelled fertilizer application) there was no significant difference in the recovery of KCl-extractable mineral N between $^{15}NO_3^-$- and $^{15}NH_4^+$-treated simulated-grazing treatments (Table 4.5).

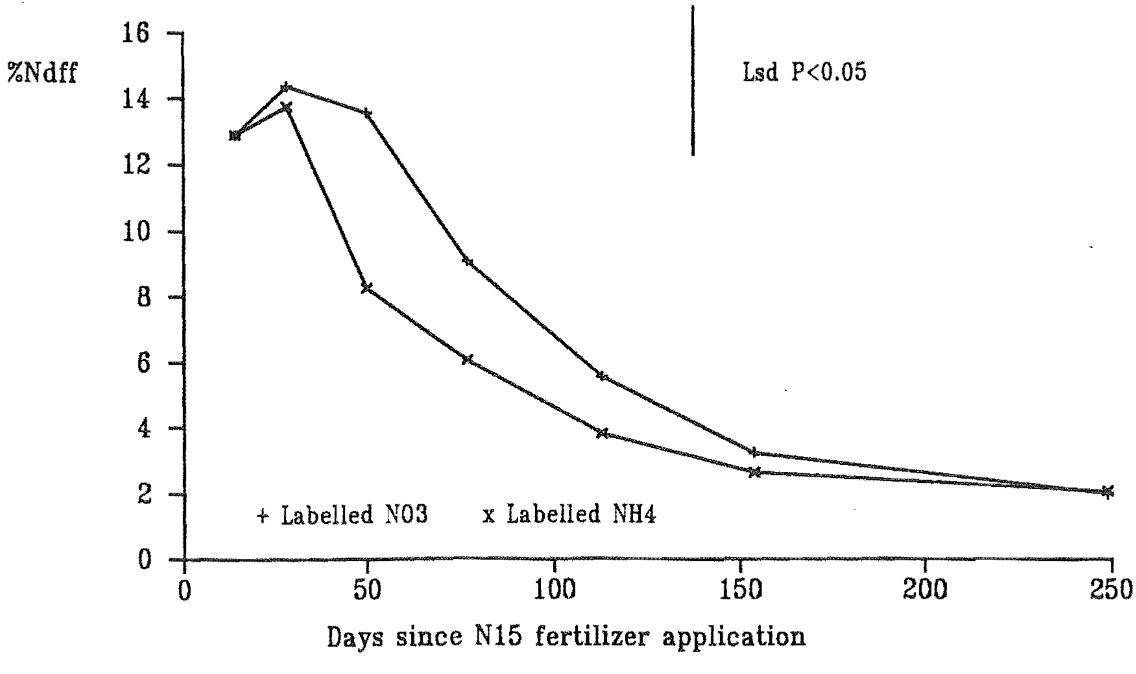


Figure 4.2 **Proportion of nitrogen derived from ^{15}N-labelled fertilizer in pasture clippings, September 1988-May 1989.**

There is little evidence of a large sampling error given the low errors for total ^{15}N recovery in soils (Appendix 4.1a), but ^{15}N recovery at the final harvest in pasture roots and stubble did represent five percent of total ^{15}N recovery for the final harvest and this indicates that there may have been considerable interchange between roots and the soil over this period.

4.3.2 Fertilizer recovery in simulated-grazing treatment

Percent ^{15}N recovery in clipped pasture is the product of N content x %Ndff expressed as percent of N applied and is calculated using Formula 4.3.

Formula 4.3 $$\%^{15}N \text{ recovery} = \frac{\%N \times \text{biomass (g)} \times 100 \; \frac{(c - b)}{(a - b)}}{\text{weight N applied (g)}}$$

Where a, b and c are as in Formula 4.1. Pasture biomass was that determined in Section 3.3.1; weight N applied refers to g of N applied at time of ^{15}N application.

There was a significant ($P < 0.05$) interaction between sampling date and form of applied N (Fig. 4.3, Appendix 4.4). Uptake of ^{15}N-labelled fertilizer by pasture was rapid (Fig. 4.3). More $^{15}NO_3^-$ than $^{15}NH_4^+$ was recovered in pasture after 14 days and by 28 Days after fertilizer application, 32% of the $^{15}NO_3^-$ applied had been removed in pasture harvested compared to 24% in the $^{15}NH_4^+$-treated plots. Between days 28 and 50 there was a marked drop in pasture dry matter production rate (Fig. 3.4) due to drought (Figures 2.1 and 2.2) and this was reflected in a dramatic drop in ^{15}N recovery.

Between 14 and 50 days after application 22.3 mm of rain fell, and during October the average relative humidity at 9.00 a.m. was 49% (S.E. = 2.66). There was also a rapid decline in soil volumetric moisture content (Chapter Eight). Pasture dry matter production was low between Days 77 and 154 due to the drought conditions (see Section 3.3.1). During this time only 133.5 mm of rain fell (Section 2.2).

A comparison of total N removed during the course of the experiment showed that significantly more $^{15}NO_3^-$ was recovered in pasture although there was no significant difference in the quantity of N and dry matter removed in successive harvests (Table 4.6). This was largely a result of the rapid uptake of NO_3^- by the pasture soon after application of ^{15}N-labelled fertilizer (Fig. 4.3).

Although the pool of total ^{15}N in the soil remained static in all these treatments (Section 4.4.2), considerable uptake by pasture and its removal in the simulated-grazing treatments occured after 26 September. This suggests that either there was considerable sampling error when sampling soils, or pasture roots may have contained considerable pools of ^{15}N at the time of the two intervening soil samplings.

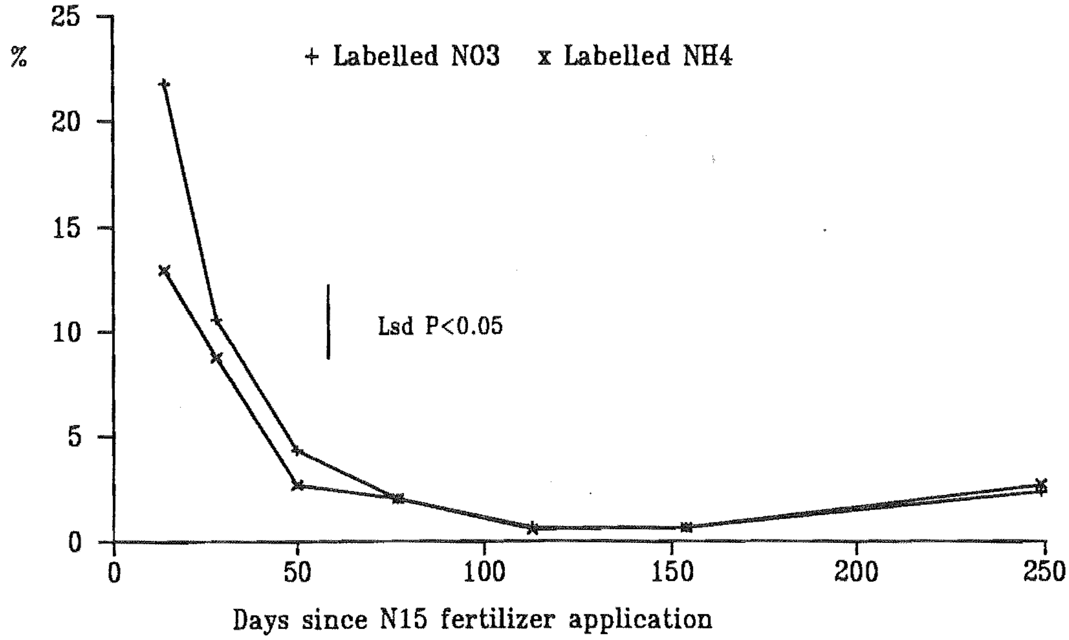


Figure 4.3 **Percent ^{15}N recovery by pasture, September 1989-May 1989.**

Table 4.6 **Cumulative ^{15}N recovery, pasture dry matter production and N removed/plot (area = 11.341 m^2), September 1988-May 1989 (n = 3).**

	Grazing			
	$^{15}NO_3^-$	$^{15}NH_4^+$	S.E.[1]	P[2]
N content (g)	155.39	142.10	22.47	0.6867
DM production (g)	3632	3452	361.1	0.7421
$\%^{15}N$ recovery	42.48	30.38	2.695	0.0193

1 Standard error.
2 Probability of treatment differences according to ANOVA.

4.4 Uptake of ^{15}N-labelled nitrogen by trees

4.4.1 Fertilizer nitrogen dynamics in needles

The uptake of ^{15}N by fertilized trees was examined by monitoring needle N content, %Ndff and needle ^{15}N content. The dynamics of these were followed by sampling foliage 14, 50, 113, 154 and 249 days after the labelled N application. Samples were analyzed for current, one- and two-year-old needles in three positions in the crown; uppermost crown, upper crown and lower crown.

Needle N content of fertilized trees was calculated using needle weight (Section 2.5.5) and needle N concentration.

4.4.2 Total nitrogen content per needle

All data were analyzed after logarithmic transformations to equalize treatment variances of the mean. Untransformed means are presented graphically.

The N content of one-year-old needles was not significantly different 14 days after ^{15}N application (Appendix 4.5a). This suggests that the pasture treatments imposed the previous April had not altered the pattern of accumulation of N into foliage of the plus-N treatments over the winter. However, N content of current needles in the upper crown of sprayed trees was significantly higher ($P < 0.05$) and needle N content was 56% greater than in the plus-pasture treatments.

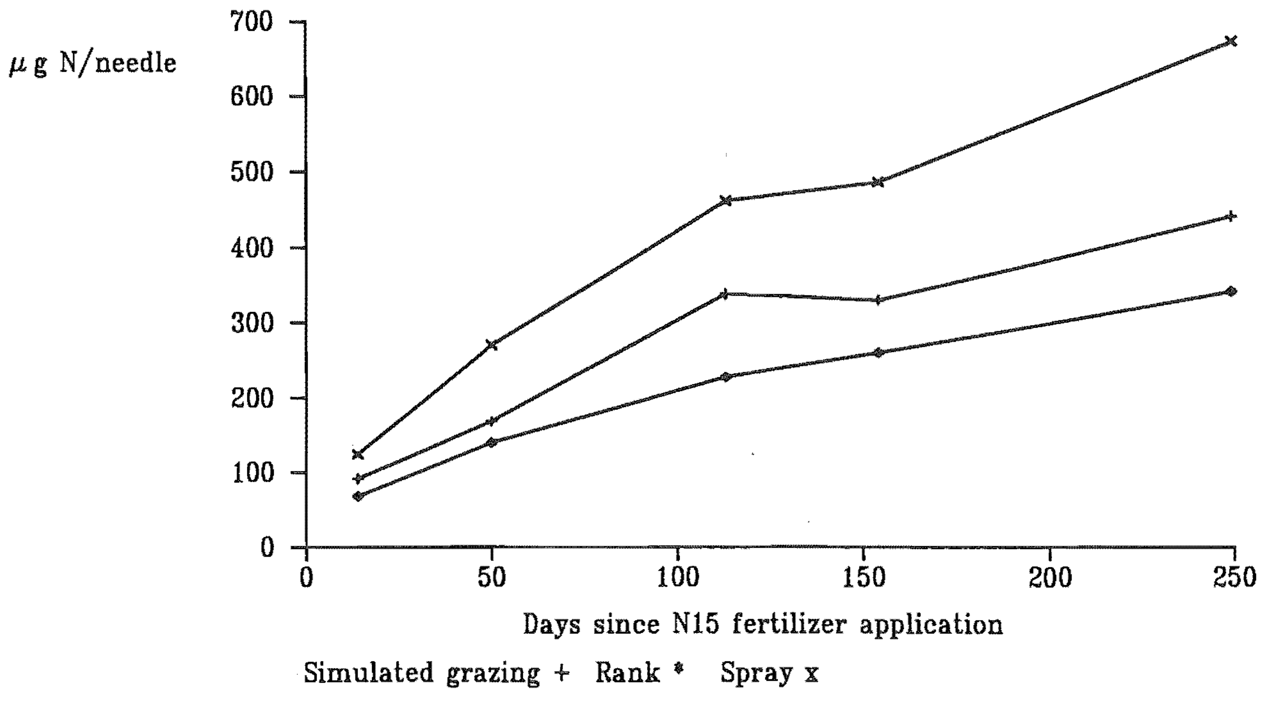


Figure 4.4 **Seasonal pattern of individual needle nitrogen content in current needles in the upper crown, September 1988-May 1989.**

Nitrogen content of two-year-old needles in the lower crown showed a significant treatment x sampling date interaction (Appendices 4.6a and 4.7). Needle N content of the sprayed treatment decreased the greatest amount.

There were no other significant ($P < 0.05$) treatment x time interactions for changes in needle N content (Appendix 4.8a). However, this interaction was almost significant at $P = 0.0875$ and $P = 0.0585$, respectively, for current needles in the uppermost and upper crown.

The removal of pasture competition resulted in significant ($P < 0.05$) treatment effects for current needles in the upper and lower crown positions with more N occurring in these needles in the sprayed treatment than in the pasture treatments (Appendix 4.8a).

One-year-old needles did not show any significant treatment effects but their N content in all treatments did decrease with time (Appendix 4.7).

The effect of the presence of pasture was to reduce tree uptake and this became very apparent within 50 days of current needle expansion.

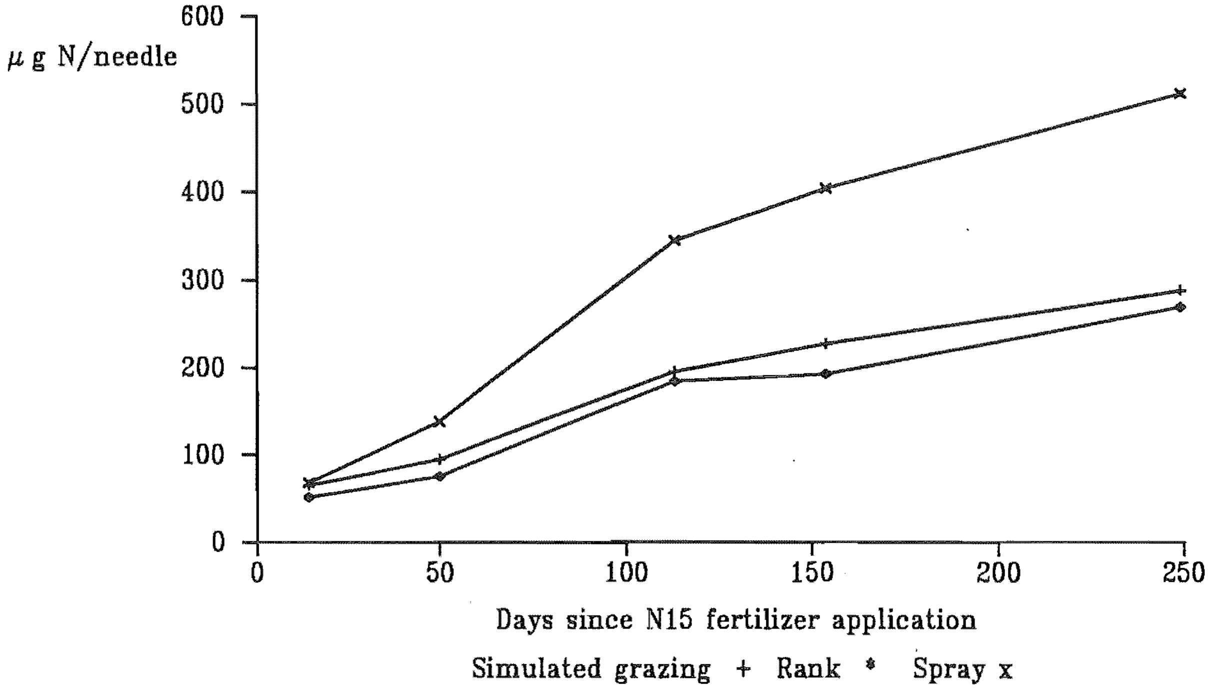


Figure 4.5 **Seasonal pattern of individual needle nitrogen content in current needles in the lower crown, September 1989-May 1989.**

Current and one-year-old needles exhibited significant ($P < 0.05$) changes in N content from one sampling date to another (Appendices 4.8a and 4.7). Total N content in current needles (Figures 4.4 and 4.5) increased over the length of the experiment whereas total N content of one-year-old needles declined significantly with time (Appendices 4.7).

At the final harvest, 249 days after application of ^{15}N-labelled fertilizer, total N content of one- and two-year-old needles was not significantly different between treatments with and without pasture whereas N content of current needles in the sprayed treatment was significantly higher than in those treatments with competing pasture ($P < 0.604$) (Appendix 4.9a). However, one-year-old needles in the upper crown in the simulated-grazing treatment contained more N than those in the rank treatment ($P < 0.05$) (Appendix 4.9a).

4.4.3 Proportion of nitrogen derived from the ^{15}N-labelled fertilizer in needles

^{15}N-labelled fertilizer was detected in all treatments when needles were first sampled 14 days after ^{15}N application. In general, at 14 days, current needles in the uppermost crown had lower %Ndff than current needles in the lower crown. There were similar levels of %Ndff in one-year-old needles in lower and upper crown positions but %Ndff was higher in current needles than in older needles (Appendices 4.5b and 4.10).

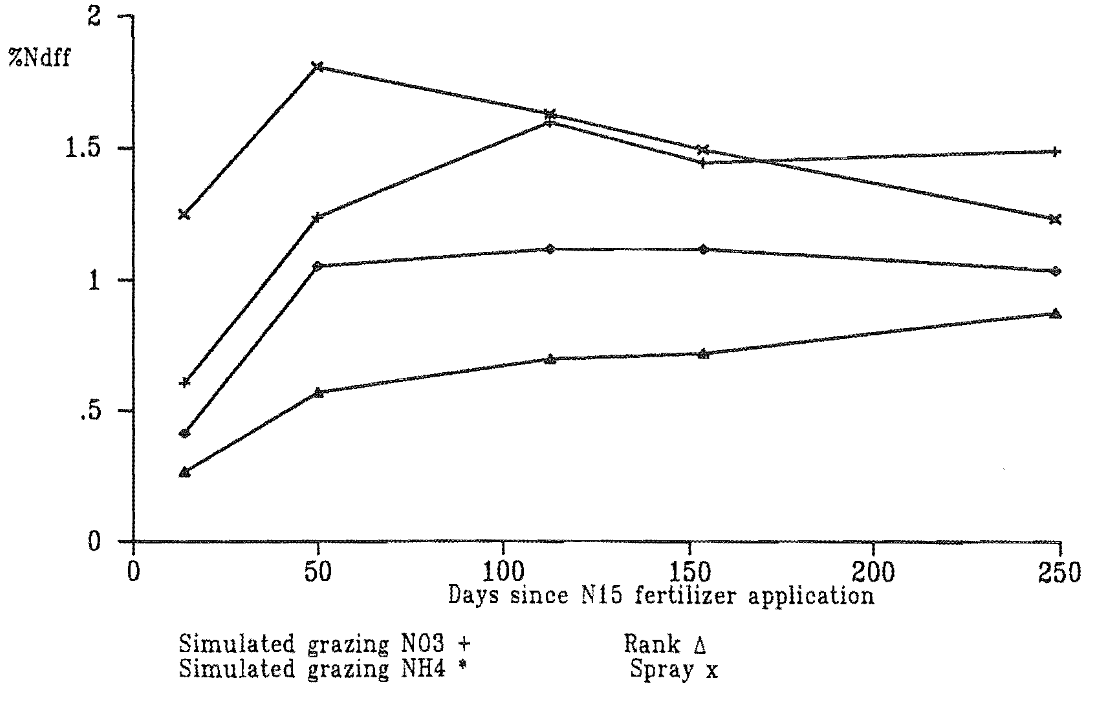


Figure 4.6 Seasonal pattern of %Ndff for current needles in the upper crown, September 1988-May 1989.

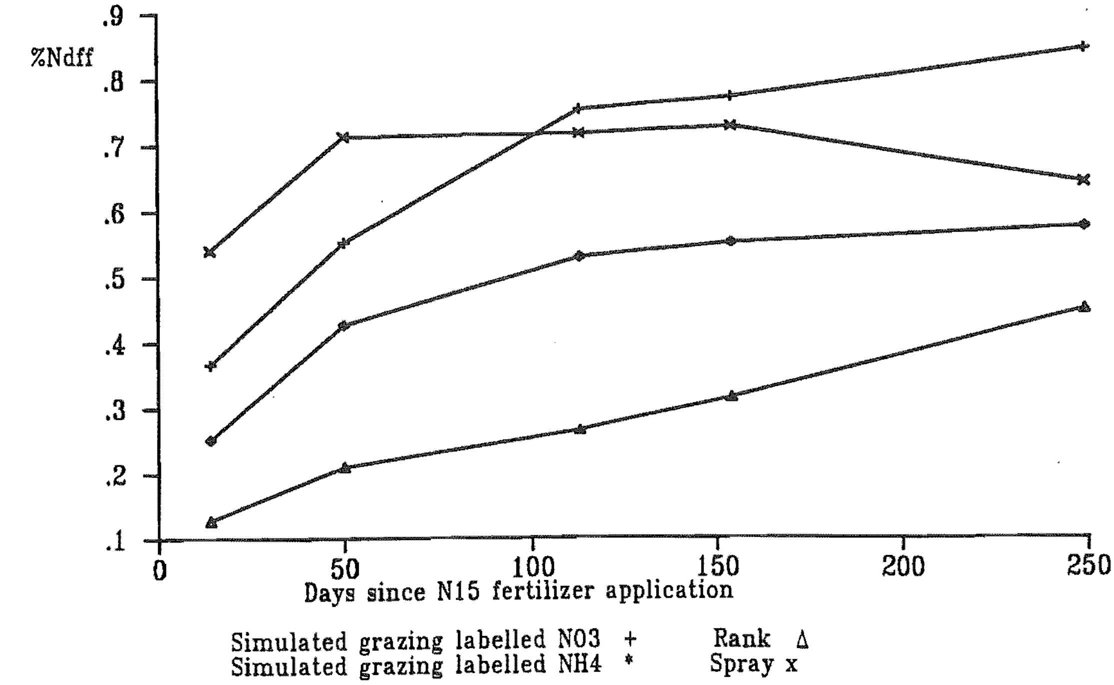


Figure 4.7 **Seasonal pattern of %Ndff for one-year-old needles in the upper crown, September 1988-May 1989.**

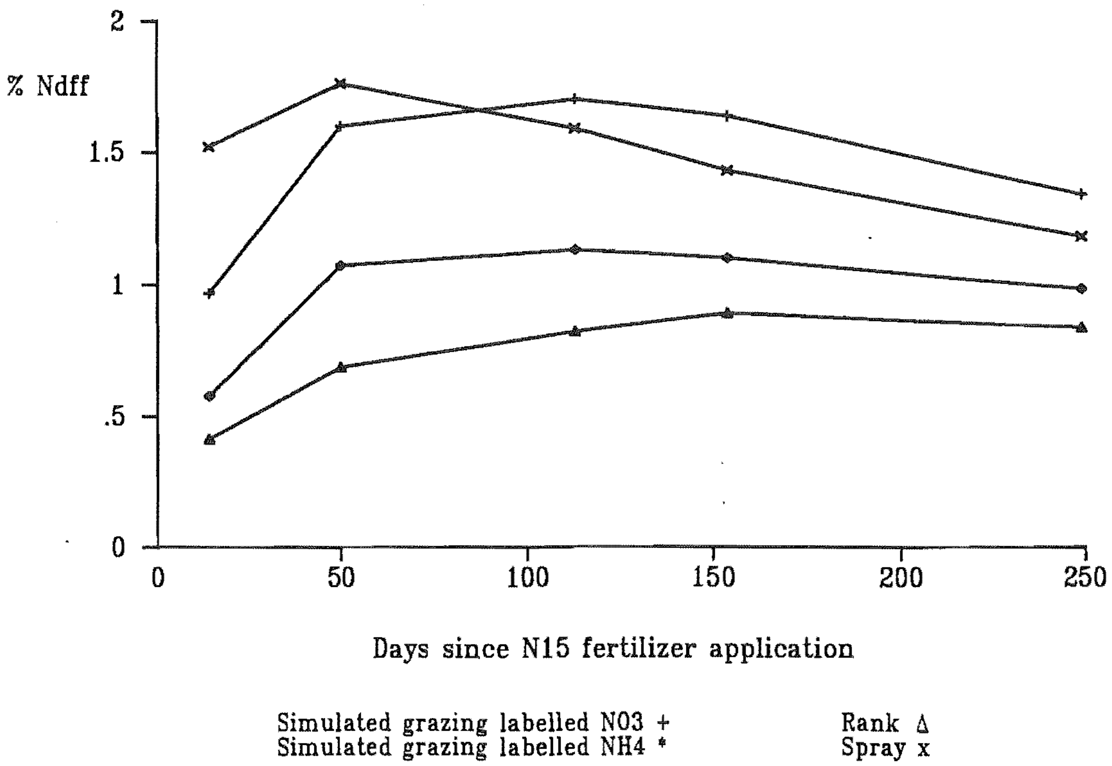


Figure 4.8 **Seasonal pattern of %Ndff for current needles in the lower crown, September 1988-May 1989.**

The %Ndff in current, one- and two-year-old needles in the sprayed treatment was significantly higher ($P < 0.1$) than in treatments with competing pasture (Appendix 4.5b) at 14 days after ^{15}N-labelled fertilizer application. At the final harvest, 249 days after application, there were no significant treatment effects ($P < 0.1$) (Appendix 4.9b). Uptake of ^{15}N-labelled fertilizer as a proportion of total uptake was apparently similar amongst the treatments. There was a significant ($P < 0.05$) treatment x time interaction for %Ndff in current and one-year-old needles in the upper crown (Figures 4.6 and 4.7, Appendix 4.8b), and current needles in the uppermost crown (Appendices 4.8b and 4.10) but there were no other significant ($P < 0.05$) treatment x time interactions (Appendices 4.8b and 4.6b).

The removal of pasture competition resulted in significant ($P < 0.05$) treatment effects for current and two-year-old needles in the lower crown and on average was 42% and 63% higher, respectively, in the sprayed treatments (Appendices 4.6b and 4.8b). Labelling in older foliage continued to increase until Day 154, with either a further increase or a slight decline up until the end of the experiment (Figures 4.7 and 4.8). The %Ndff generally peaked in the current foliage in the sprayed treatments first and then in the simulated-grazing treatments. %Ndff in the simulated-grazing treatment is generally higher in the trees treated with $^{15}NO_3^-$ than $^{15}NH_4^+$ indicating the greater availability of $^{15}NO_3^-$. The %Ndff in current and one-year-old needles in the rank-plus-N treatments increased throughout the length of the experiment, and only in current needles in the lower crown at the final sampling did dilution of fertilizer ^{15}N occur.

4.4.4 ^{15}N fertilizer content per needle

The ^{15}N content of needles is the product of needle N content and the proportion of N derived from ^{15}N-labelled fertilizer. There was a significant ($P = 0.0132$) treatment x time interaction for ^{15}N content of current needles in the upper crown (Fig. 4.9, Appendix 4.8c). This interaction was the result of needles in the sprayed treatment initially accumulating higher quantities of ^{15}N than the other treatments (Fig. 4.8) and, later while ^{15}N contents in other treatments increased, ^{15}N content of needles in the sprayed treatment decreased. There were no other significant treatment x time interactions ($P < 0.05$) (Appendices 4.6b, 4.7c, and 4.11).

Except for one-year-old needles in the lower crown, needle ^{15}N content in current and one-year-old needles showed significant changes ($P < 0.05$) from one sampling date to another (Appendix 4.8c). For example, current needles in the upper crown and lower crown rapidly accumulated ^{15}N until Day 113 after ^{15}N application (Figures 4.9 and 4.10, respectively). All treatments then showed a slight decrease at the next sampling, but after that ^{15}N content increased again. The treatment x time interaction was significant for one-year-old needles in the upper crown (Fig. 4.11, Appendix 4.8c), and current needles in the lower crown ($P = 0.0846$ and $P = 0.0843$, respectively) (Fig. 4.10). The main treatment effects showed the removal of competing vegetation significantly ($P < 0.05$) increased the ^{15}N content of all current needles and one-year-old needles in the

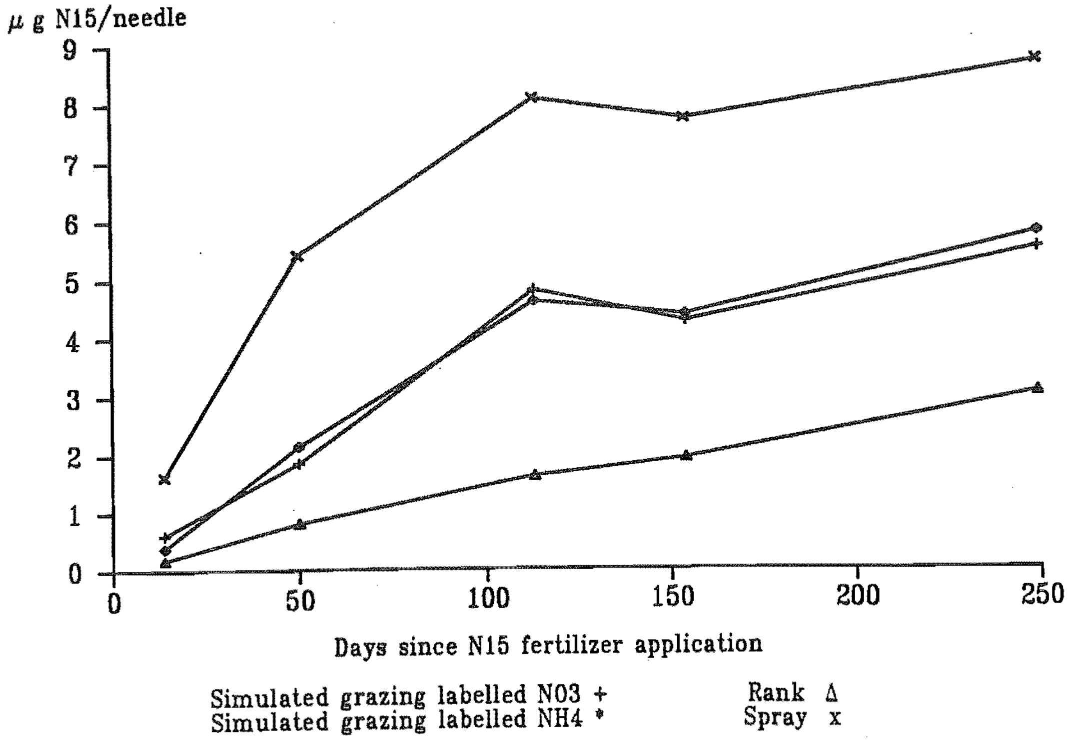
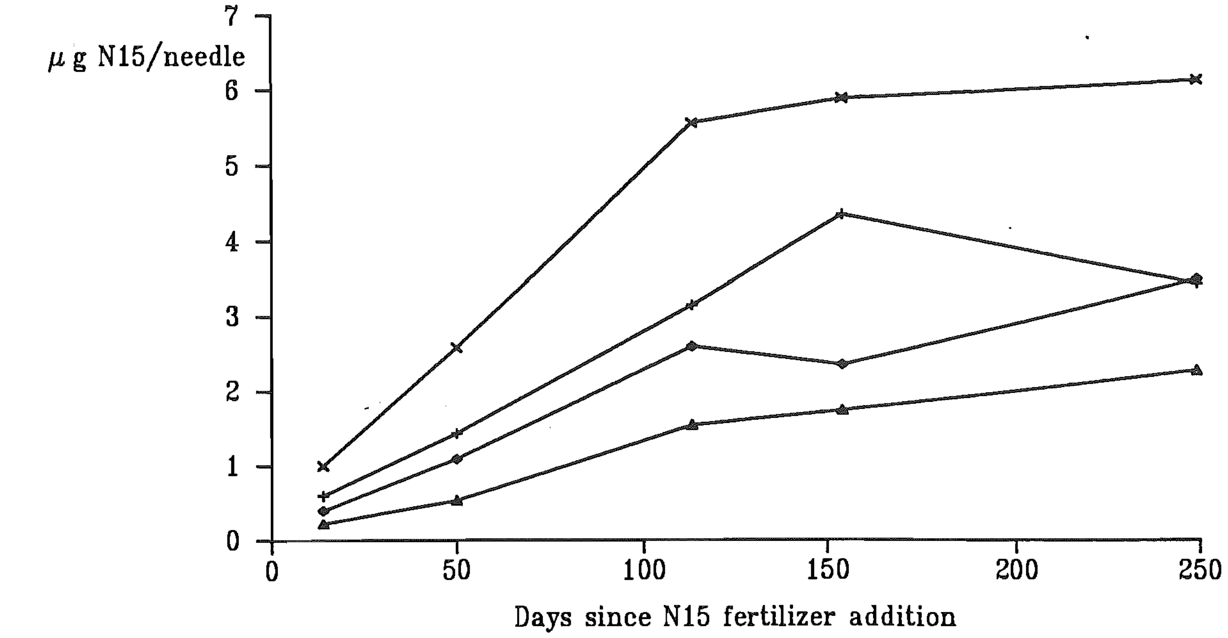


Figure 4.9 **Seasonal pattern of individual needle ^{15}N content in current needles in the upper crown, September 1988-May 1989.**

upper crown (Appendix 4.8c). The simulated-grazing treatment significantly increased ($P = 0.0402$) the ^{15}N of one-year-old needles in the upper crown compared to those in the rank treatment. This was the only needle class showing such a response. There were no significant differences between $^{15}NO_3^-$ and $^{15}NH_4^+$ forms of N (Appendices 4.6b and 4.8c).

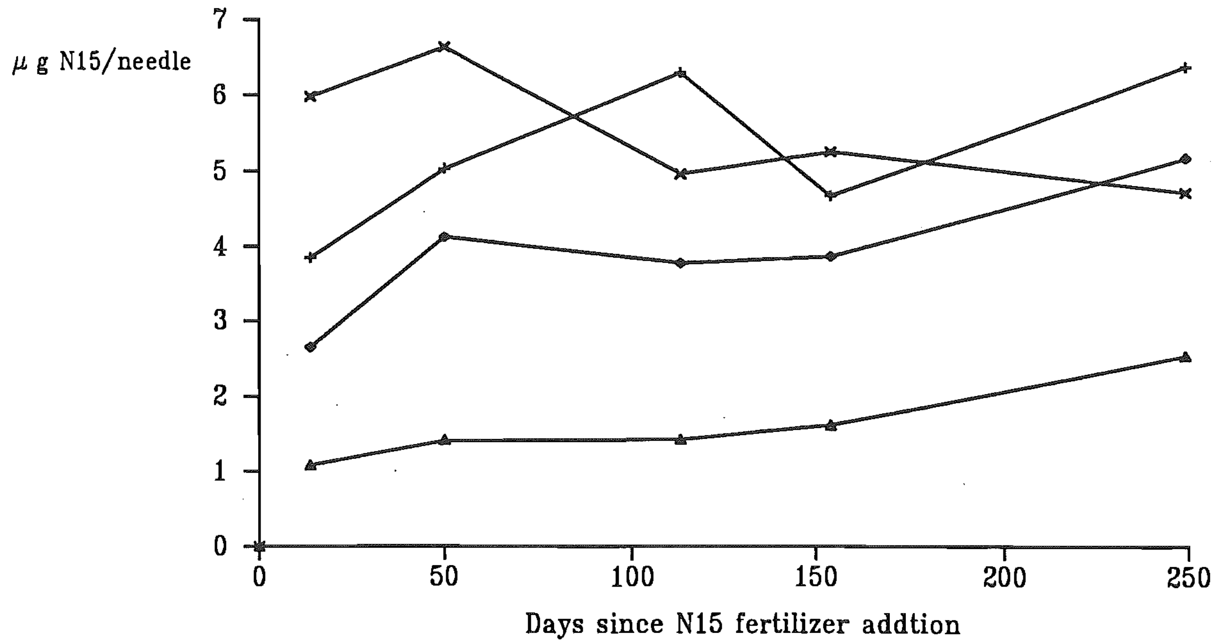
The ^{15}N content in current, one-year-old and two-year-old needles in the sprayed treatments was significantly higher ($P < 0.01$) than in treatments with competing pasture (Appendices 4.5c and 4.6b) at 14 days after ^{15}N-labelled fertilizer application. At the final harvest, 249 days after application, ^{15}N content of one- and two-year-old needles was not significantly different between treatments with and without pasture whereas current needles in the sprayed treatment were significantly higher in ^{15}N than those in treatments with competing pasture ($P < 0.1$) (Appendix 4.9c).

However, at the end of the experiment one-year-old needles in the upper crown of the simulated-grazing $^{15}NH_4^+$ treatment contained significantly more ^{15}N ($P = 0.0867$) than those in the rank treatment. Two-year-old needles in the lower crown of trees in the simulated-grazing-plus-$^{15}NO_3^-$ treatment contained significantly more ^{15}N ($P = 0.0811$) than those in the $^{15}NH_4^+$-labelled treatment (Appendix 4.9c).



Simulated grazing labelled NO3 + Rank Δ
Simulated grazing labelled NH4 * Spray x

Figure 4.10 **Seasonal pattern of individual needle ^{15}N content in current needles in the lower crown, September 1988-May 1989.**



Simulated grazing labelled NO3 + Rank Δ
Simulated grazing labelled NH4 * Spray x

Figure 4.11 **Seasonal pattern of individual needle ^{15}N content in one-year-old needles in the upper crown, September 1988-May 1989.**

The effect of the spraying treatment on ^{15}N uptake by *P. radiata* became apparent very early after ^{15}N application. Fourteen days after ^{15}N application current needles in the lower crown of the sprayed treatment contained almost four and one half times more ^{15}N than similar needles in rank treatments. However, there were nearly no differences in total needle N (68 and 52 μg N, respectively) between these two treatments (Fig. 4.11). Between Days 14 and 50, total N content increased by 60% on average, whereas ^{15}N content increased by 141% on average.

The ^{15}N content of current needles in the lower crown of all treatments, except for the simulated-grazing plot treated with $^{15}NO_3^-$, continued to increase from Day 154 until the final harvest. In the latter treatment ^{15}N content apparently declined.

At Day 154 those needles in the sprayed treatment contained 96% of their final ^{15}N content, therefore, further uptake of ^{15}N was minimal in a period when ^{15}N levels in mineral N were still relatively high compared with other treatments.

In this same period %Ndff in these needles decreased by 18% while total N content continued to increase by 27%. This suggests that trees in the sprayed treatment were taking up proportionally more unlabelled N. This is consistent with the general trend of %Ndff in all classes of needles on sprayed trees (Appendix 4.10).

Between Day 154 and the final harvest, ^{15}N content of current needles in the lower crown increased by 33 and 24% in the $^{15}NH_4^+$-treated simulated-grazing and rank treatments, respectively. This trend demonstrates that in these treatments ^{15}N was still available for tree uptake.

It is possible that the decrease in ^{15}N content in current needles in the lower crown of the $^{15}NO_3^-$-treated simulated-grazing treatment was due to the re-translocation of $^{15}NO_3^-$ stored in these needles to current and one-year-old needles in the upper and uppermost crown, given that the ^{15}N content of these needles increased during this same period.

It is not possible to extend the conclusions of this analysis to a whole tree basis as the analysis refers to particular foliage components. Differences in ^{15}N uptake and accumulation in other tissues may have occurred between treatments.

It is important to remember that the comparison of treatments using per needle parameters requires that all treatments have equal numbers of needles. For this study this assumption was found to be true (Section 3.5).

4.4.5 ^{15}N in older foliage and senescent needles

In early March 1989 two-year-old or older yellow senescent needles, either still attached to branches or sitting loosely amongst otherwise attached needles, were collected from the mid-crown position.

Removal of competition between *P. radiata* and pasture significantly increased the %Ndff in senescing needles ($P < 0.05$) (Table 4.7) by 114% (Appendix 4.12). The %Ndff was considerably lower than in two-year-old needles in the lower crown sampled earlier in February or at the end of the experiment (Appendices 4.9b and 4.10).

Table 4.7 %Ndff, nitrogen content and ^{15}N content of senescing needles collected on 8 March 1989.

Grazing		Rank	Spray		
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]	P[2]
		%Ndff			
0.0818	0.0662	0.0728	0.1577	0.02829	0.1574
		μg N per needle			
72.64	106.70	101.09	90.73	16.115	0.4988
		μg ^{15}N per needle			
0.0566	0.0808	0.0649	0.1348	0.0259	0.2177

1 Standard error.
2 Probability of treatment differences according to ANOVA.

This suggests that although there was considerable removal of total N and ^{15}N in two-year-old needles (Table 4.7, Appendices 4.8 and 4.11), not all ^{15}N taken up is re-translocated from these needles. ^{15}N is, however, re-translocated in a higher proportion, thus resulting in the decreased %Ndff in the senescent needles.

4.5 Summary

- The pool of ^{15}N in total soil N remained relatively constant after 154 days following ^{15}N application.

- Soil availability and plant uptake depend on the form of ^{15}N applied and level of pasture competition. $^{15}NH_4^+$ is rapidly immobilized in the rank and simulated-grazing treatment and pasture uptake of $^{15}NH_4^+$ is significantly lower than $^{15}NO_3^-$. Removal of pasture competition increased *P. radiata* ^{15}N uptake and increased ^{15}N recovery in KCl-extractable mineral N as well as the proportion of ^{15}N as $^{15}NO_3^-$.

- Recovery of ^{15}N by pasture was negatively affected by the dry conditions during late September and October.

- ^{15}N was equally available in soil in all treatments (Section 4.2.1). However, %Ndff does not indicate the size of the pool of available ^{15}N, but only that ^{15}N is available throughout the length of the experiment (also confirmed by the KCl-extractable mineral N data, Section 4.2.5). Therefore, the dynamics of total needle N are important in the understanding of ^{15}N uptake because they indicate fluxes in the quantity of total N taken up.

- In assessing the competitive interaction between *P. radiata* and pasture it is important to assess the ^{15}N content of needles in relation to total N taken up. There were differences in the uptake of total N into needles, especially into current needles in the lower crown.

- There is good evidence that most of the ^{15}N uptake occurred early in the study. However, there is no indication that uptake of ^{15}N by *P. radiata* had completely ceased before the final harvest. This may only be established conclusively by the use of sequential harvests as used by Nambiar and Bowen (1986). At the time of harvest, ^{15}N was still present in plant-available mineral N and ^{15}N was still being taken up by pasture in the simulated-grazing treatment.

- Low uptake of ^{15}N into the *P. radiata* canopy may reflect immobilization and competition for N in the $^{15}NH_4^+$-treated simulated grazing and rank treatments respectively. In these treatments it is possible that $^{15}NH_4^+$ was initially rapidly immobilized given the low levels recovered in mineral N (Section 4.2.5) and was subsequently slowly released. In the plots that received $^{15}NO_3^-$, $^{15}NO_3^-$ remained available to trees for a longer period and was only slowly immobilized. In the rank treatment both competition for and immobilization of $^{15}NH_4^+$ are important mechanisms that reduce pasture and tree uptake.

- Uptake by pasture in the simulated-grazing treatment did not seem to reduce ^{15}N movement into the canopy to the same extent as uptake by rank pasture. There is no apparent reason for this except that the simulated-grazing treatment, with return of N, may have bestowed a benefit upon tree uptake of ^{15}N.

- Retranslocation of ^{15}N from senescing foliage occurs.

Chapter Five

Nitrogen uptake and distribution

5.1 Introduction

The effect of various levels of vegetation management on *P. radiata* growth was described in Chapter Three. In this chapter, one of the possible mechanisms for the observed differences in growth of *P. radiata* due to different vegetation management practices will be addressed. This mechanism is competition for N. These dynamics were assessed using the stable ^{15}N isotope techniques.

Nitrogen removed at successive harvests of the simulated-grazing treatment was calculated from biomass data (Chapter Three). The amount of N in the rank pasture and in the trees was assessed at the end of the experiment.

5.2 Nitrogen uptake into pasture in the simulated-grazing treatment

Nitrogen removal in the simulated-grazing and grazing-plus-N treatments was assessed on 11 occasions during the experiment. The quantity of N removed from plots at the initial pre-treatment harvest was used as a covariate in the analysis of these data.

Repeated measures analysis of variance indicated that there were significant changes in the quantity of N removed from the simulated-grazing treatment from one sampling date to another over all treatments, and the treatment x time interaction was also significant ($P = 0.0345$) (Fig. 5.1, Appendix 5.1).

The major simulated-grazing harvest was in the early spring before the drought had an impact and in the following autumn (Fig. 5.1). Thus, in the plus-N treatment, N removed in clippings in the 26 September 1988 harvest accounted for 24.8% of the total N removed during the experiment and 41.5% of the quantity of N added to that date. In contrast, in the no-N treatment, the N removed in clippings in the 26 September harvest accounted for 29.8% of total N eventually removed (Fig. 5.1).[1] Before 10 October, 46% of the total amount of N eventually removed had been removed.

1 The simulated-grazing-no-N plots did not receive their first return of N from clippings until 10 October.

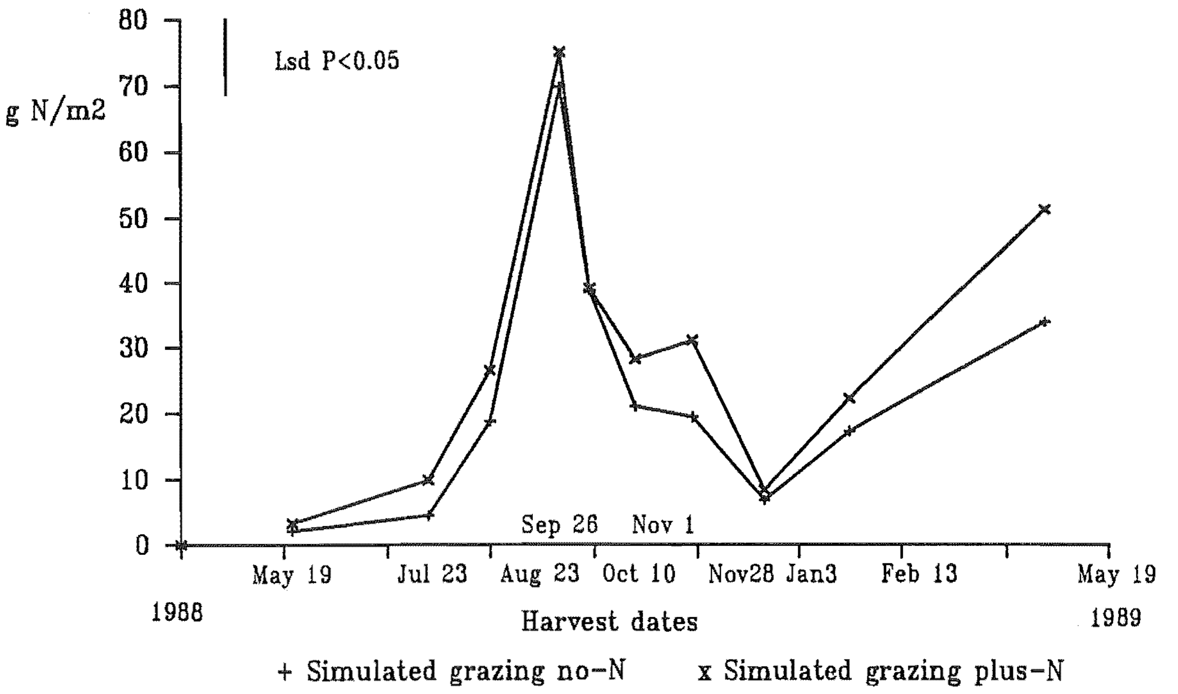


Figure 5.1 Nitrogen removal from simulated-grazing treatment, May 1988-May 1989, adjusted for initial harvest differences in March 1988.

By the end of the experiment the cumulative amount of N removed from the no-N treatment was approximately 80% of that removed from the plus-N treatment, yet these plots received less than 22% of N added to plus-N plots. It is possible that the difference between total N removed and N additions of 141 kg N/ha in the no-N treatment represents biological N fixation. Further evidence for this phenomenon is seen in Chapter Seven which shows that net N mineralization was very low in the no-N treatment and that this process does not account for the increased N in the no-N simulated-grazing treatment. Given that plots in the no-N treatment had a good cover of clover it is probable that biological N fixation was responsible for the high amounts of N removed in the September and October harvests.

The total addition of N to the simulated-grazing-no-N treatment was about half the total quantity removed from the plots (Appendix 2.2). In the plus-N treatment only one third of the quantity removed in the harvests was returned to the plots. Generally, by the end of the experiment, removal in the plus-N plots accounted for 70% of total N added in the monthly N additions and returns of N removed by simulated-grazing.

Thus, the methodology of using N concentrations determined for pre-treatment harvest and returning 80% of N removed (Quinn, 1982) resulted in the quantity of N removed being underestimated (Appendix 2.2) and consequently that less N than originally planned was returned. Thus, the grazing treatment was harsher in terms of N removal than intended.

5.3 Nitrogen concentration of *P. radiata* biomass components

The N concentration in the *P. radiata* biomass components at the final harvest was analyzed using ANOVA (Table 5.1, Appendix 5.2). There were no significant interactions ($P < 0.05$) between the level of vegetation management and the application of N, except in the buds (Fig. 5.2).

In all treatments, except the spray-plus-N, total N concentration of buds increased with the monthly addition of N. The application of N to rank pasture did not greatly increase N concentration in buds but N application to the simulated-grazing treatment increased %N concentration by 26% and this was probably due to accumulation of N in the simulated-grazing treatment. Total N concentration in buds in the sprayed-plus-N treatment may have been lower due to dilution in the tissues while there may have been a slight accumulation in the spray-no-N treatment. Total N concentration of buds was reduced by the simulated-grazing treatment but increased by seven percent with the removal of competing vegetation.

The application of N significantly ($P < 0.05$) increased the concentration of N in older branches, current wood and older wood, and current bark (Appendix 5.2). On average, these rose by 14.8, 20 and 33, and 32% respectively.

The level of competing vegetation also significantly altered the N concentration. For several components, notably current needles in the lower crown, current branches, current wood and bark, N concentration was significantly higher ($P < 0.05$) in the simulated-grazing treatment than in the rank treatment, and there were no significant differences ($P < 0.05$) between sprayed treatments and other treatments. Thus, simulated-grazing increased N concentrations in these components but spraying did not. Presumably this was due to the increased rate of nutrient cycling created by simulated-grazing with return of some N removed in clippings.

5.4 Needle nitrogen content at final harvest

Needle N content was calculated using individual needle weight data from the 27 April 1989 needle collection and total N concentration of needle samples from the final harvest; data were analyzed using ANOVA (Appendix 5.3). There were no significant interactions ($P < 0.05$) between the level of competing vegetation and added N. However, removal of competition by spraying significantly increased the N content of current needles in the upper ($P = 0.0002$) and uppermost crown ($P = 0.0339$) with the biggest increases detected in current needles in the lower crown ($P = 0.0001$) (Table 5.2, Appendix 5.3).

Table 5.1 Total nitrogen concentration in *P. radiata* biomass components and pasture roots at the final harvest.

	Grazing		Rank		Spray		
Tree components	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			% dry weight				
Needles[2]							
CNUMC	2.10	1.64	1.78	1.63	1.73	1.78	0.122
CNUC	1.92	1.61	1.64	1.51	1.65	1.71	0.094
Y1UC	1.58	1.35	1.32	1.25	1.41	1.44	0.079
CNLC	1.68	1.63	1.55	1.47	1.59	1.69	0.055
Y1LC	1.33	1.36	1.24	1.18	1.36	1.42	0.055
Y2LC	1.04	1.01	0.99	0.94	1.05	1.10	0.049
Branches							
Current	0.69	0.54	0.59	0.58	0.57	0.59	0.053
Older	0.32	0.26	0.30	0.23	0.31	0.32	0.022
Stem							
Current	0.31	0.24	0.23	0.19	0.25	0.23	0.017
Older	0.17	0.11	0.14	0.11	0.13	0.11	0.009
Bark							
Current	1.69	1.06	1.02	0.87	1.10	0.96	0.131
Older	0.70	0.57	0.52	0.54	0.67	0.66	0.046
Roots							
Fine roots[3]	1.38	1.08	1.07	0.99	1.05	1.09	0.080
Coarse roots	0.41	0.35	0.36	0.28	0.40	0.44	0.040
Stump	0.30	0.24	0.27	0.22	0.29	0.28	0.023
Pasture roots[4]	2.09	2.25	1.93	1.78	-	-	0.120
Buds	2.22	1.74	1.86	1.81	1.53	1.86	0.122

1 Standard error.
2 KEY
- CNUMC Current needles uppermost crown
- CNUC Current needles upper crown
- Y1UC One-year-old needles upper crown
- CNLC Current needles lower crown
- Y1LC One-year-old needles lower crown
- Y2LC Two-year-old needles lower crown

3 Roots < 1 mm diameter.
4 Includes stubble and roots.

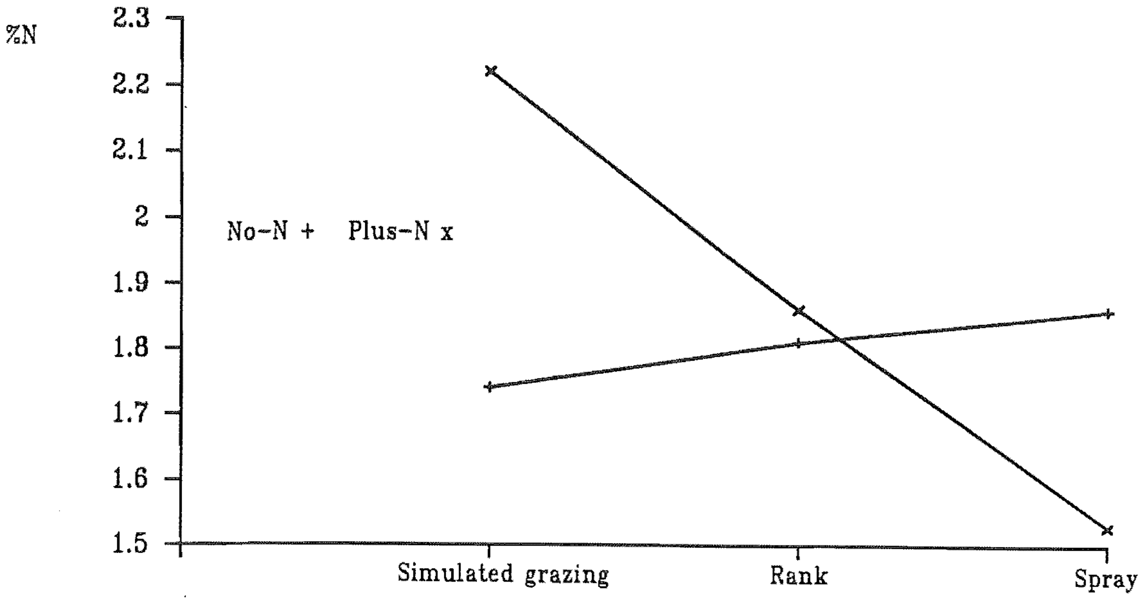


Figure 5.2 **The effect of pasture management and added nitrogen on total nitrogen concentration in current buds collected in May 1989.**

Table 5.2 **Nitrogen content of needles at final harvest.**

	Grazing		Rank		Spray		
Needle class[1]	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[2]
			(μg N/needle)				
CNUMC	654	391	445	385	793	563	112.7
CNUC	451	328	278	242	723	470	65.3
Y1UC	802	623	436	550	706	678	101.5
CNLC	284	251	252	142	542	456	52.6
Y1LC	305	328	236	227	356	328	38.9
Y2LC	283	298	266	239	290	329	39.9

1 KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1UC One-year-old needles upper crown
CNLC Current needles lower crown
Y1LC One-year-old needles lower crown
Y2LC Two-year-old needles lower crown

2 Standard error.

These increases were equal to 84, 44 and 114%, respectively, of N content of similar current needles in the plus-pasture treatments.

Simulated-grazing significantly increased N content of current needles by 50% (P = 0.0358) in the upper crown compared with the rank treatment. Nitrogen content of one-year-old needles in the upper crown was similarly significantly increased by 45% (P = 0.0327) (Appendix 5.3). Further, monthly addition of N significantly increased needle N content in current needles in the upper and uppermost crown of *P. radiata* by 41 and 40% respectively (P = 0.0143 and P = 0.0435).

Figures 5.3a and 5.3b show that in the upper crown in the rank treatment current needles were N-limited (Weetman and Fournier, 1982) in both March and May, respectively, and that luxury uptake of N occurred in the rank-plus-N treatment. This suggests that factors such as moisture stress (i.e. non-nutrient limiting factors) were limiting needle growth. All other treatments showed an increase in N content and needle weight between the March and May samplings.

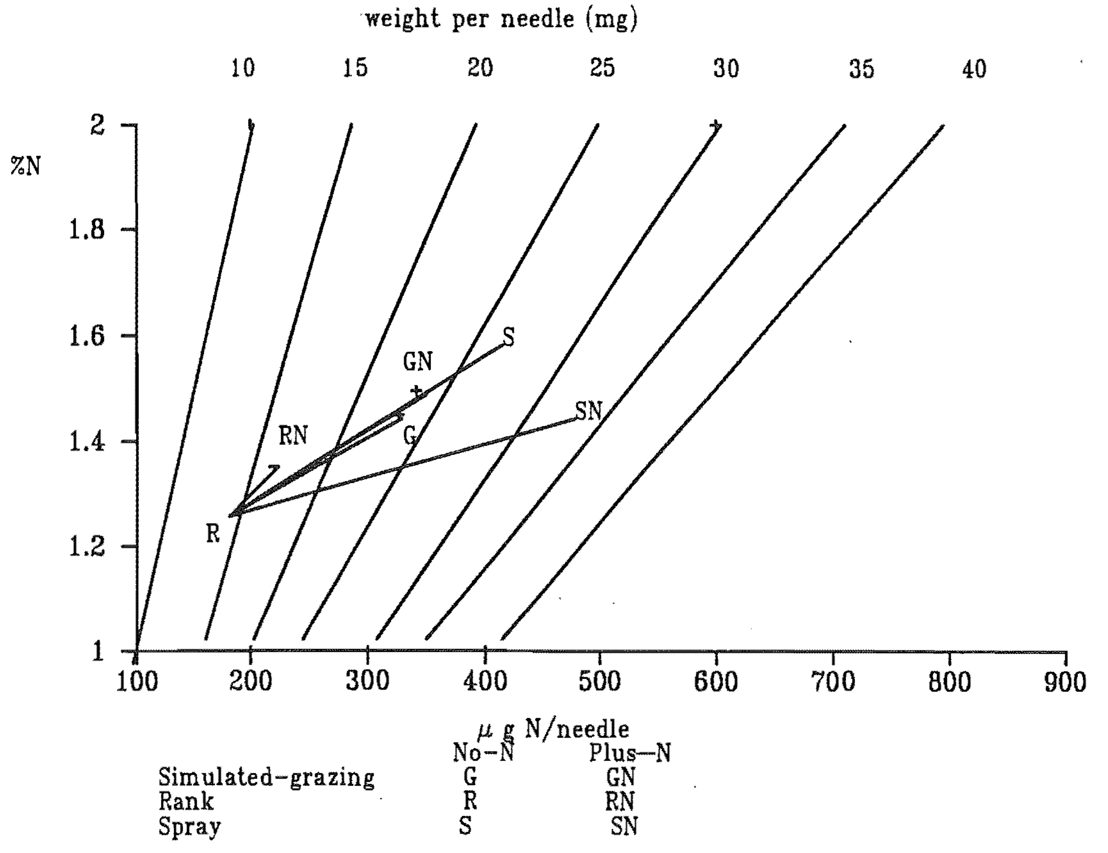


Figure 5.3a Shifts in relationship between nitrogen concentration, needle weight, and nitrogen content in March 1989.

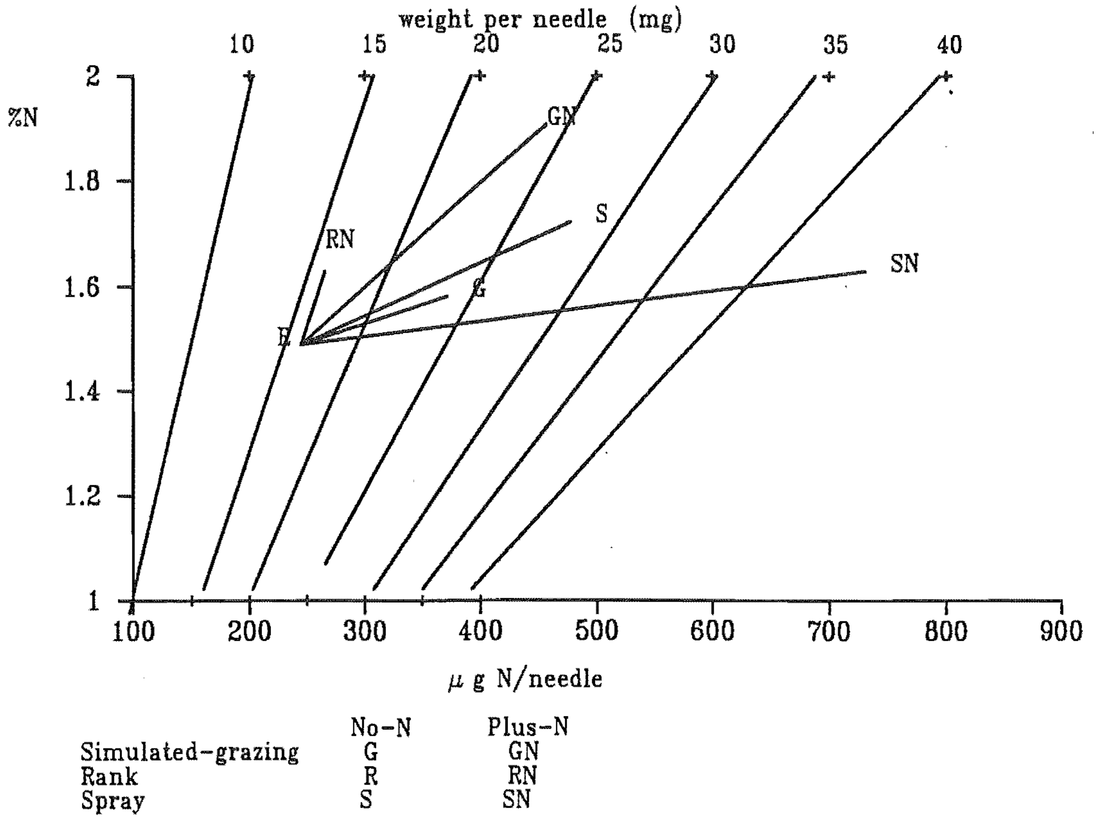


Figure 5.3b **Shifts in relationship between nitrogen concentration, needle weight, and nitrogen content in May 1989.**

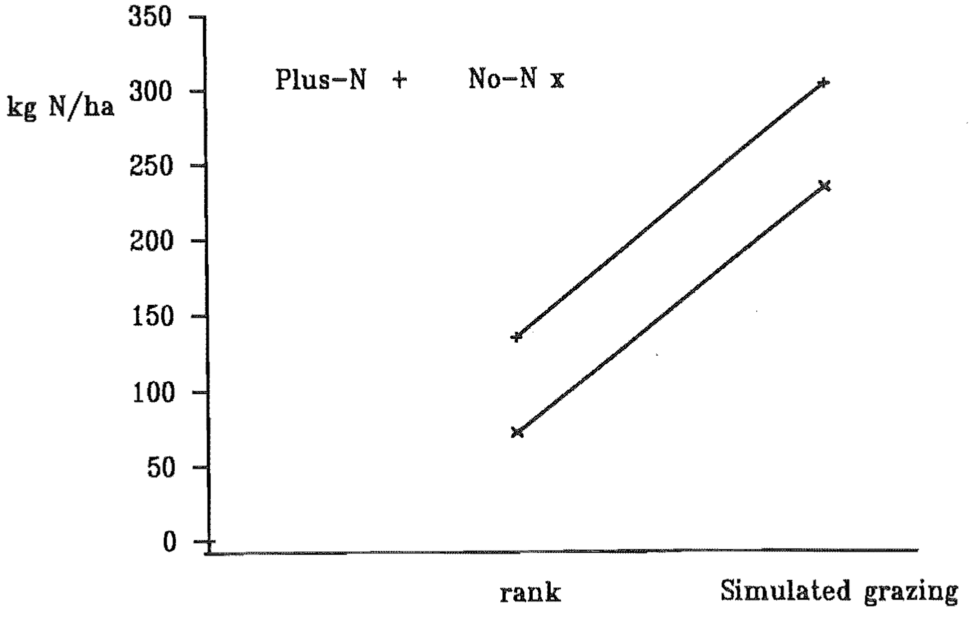


Figure 5.4 **Total nitrogen removed in the simulated-grazing and rank treatments.**

5.5 Nitrogen content of competing vegetation and trees at the final harvest

5.5.1 Nitrogen content of competing vegetation

There was no significant interaction between the level of pasture competition and added N for the total quantity of N removed in the simulated-grazing and rank treatments (Appendix 5.4a). The aboveground N content of pasture in the simulated-grazing-plus-N treatment was significantly increased ($P < 0.001$) by 159% compared with the rank treatment (Table 5.3, Fig. 5.4, Appendix 5.4a). The monthly addition of N increased aboveground N content by 43%.

Nitrogen uptake by pasture for August 1988-May 1989 as estimated by these harvests was compared with N uptake estimates obtained from harvests beneath the tree in a 1.9-m-radius circular plot with the tree at the centre for the same period for the simulated-grazing-plus-N and rank-no-N and plus-N treatments (Table 5.4). Data were analyzed using a paired T-test (Table 5.5) and the estimates were significantly different ($P = 0.0232$). The average difference between the two estimates was 7 g N/m^2 and N uptake was highest in pasture growing between trees.

Table 5.3 Total nitrogen removed in cumulative harvests of the simulated-grazing treatment and the final harvest of the rank treatment.

Grazing		Rank		
Plus-N	No-N	Plus-N	No-N	S.E.[1]
		kg/ha		
303	234	135	72	14.5

1 Standard error.

Table 5.4 Nitrogen uptake by pasture as measured at two locations relative to trees.

Plot size	Grazing		Rank		Spray	
	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N
			g/m^2			
0.5 x 0.5 m^2	25.6	20.3	13.5	7.2	0	0
1.9 m radius	13.0	10.2[1]	7.3	6.2	0	0

1 Approximately half the N content in the 0.5 x 0.5 m^2 plots.

Table 5.5 Comparison of plot location and nitrogen uptake by pasture.

0.5 x 0.5 m	1.9-m-radius plot
	$g\ N/m^2$
15.8 (8.71)[1]	8.8 (4.46)

1 Standard deviation, n = 12.

The N content belowground (stubble and pasture root) was not influenced by treatment (Table 5.6, Appendix 5.4b) and averaged 6.4 g N/m^2 beneath the trees in the 1.9-m-radius plots used for sampling tree root systems. This ranged from 103% of the aboveground N content of the rank-no-N treatment in the 1.9-m-radius plot to 49% in the simulated-grazing-plus-N treatment.

Table 5.6 Nitrogen content in pasture stubble and roots.

Grazing		Rank		
Plus-N	No-N	Plus-N	No-N	S.E.[1]
		$g\ N/m^2$		
7.0	4.4	8.4	5.8	2.06

1 Standard error.

5.5.2 Nitrogen content of trees

The N content of *P. radiata* biomass components was calculated using component oven dry weight (Section 3.4) and N concentration (Section 5.3) and statistically analyzed using initial root diameter^2 x initial height as a covariate (Appendix 5.5a).

The use of this covariate was not satisfactory (Appendix 5.5a) for the N content of pine fine roots less than 1 mm; therefore unadjusted data are presented (Table 5.7).

Table 5.7 Nitrogen content of tree biomass components at the end of the experiment, adjusted for initial tree size differences using d^2h as the covariate where appropriate.

	Grazing		Rank		Spray		
Tree components	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			g N/tree				
Foliage							
Current	105.6	80.1	107.1	61.0	197.1	181.7	18.84
1-year-old	53.5	48.3	45.0	43.8	59.2	58.6	5.94
2-year-old[2]	14.5	5.8	9.0	6.0	8.8	10.3	3.50
Total	169.0	135.9	160.0	110.1	267.4	252.1	23.13
Branches							
Current	13.5	9.54	15.6	10.3	21.7	23.7	2.79
Older	21.7	19.43	21.2	16.0	30.1	33.8	2.92
Stem							
Current	16.6	9.36	8.6	7.3	17.1	14.3	1.96
Older	8.4	4.96	6.2	4.0	5.8	4.7	0.43
Buds	5.1	2.33	4.2	3.1	8.9	10.6	2.36
Bark							
Current	1.3	0.6	0.6	0.6	1.2	1.7	0.250
Older	9.8	7.5	5.7	6.4	12.0	15.1	1.33
Total aboveground	245.6	189.5	222.2	157.7	364.0	355.9	28.8
Roots							
Fine roots[2,3]	4.0	2.4	2.1	2.5	1.9	2.5	0.670
Coarse roots	12.1	9.3	13.2	6.0	18.9	19.8	1.25
Stump	12.2	9.9	11.3	9.2	14.9	12.9	0.93
Total belowground	25.3	18.6	24.1	14.9	31.9	30.8	2.03
Total tree	277.0	207.3	234.8	168.8	412.9	379.4	31.83

1 Standard error.
2 Non-parallel slopes ($P < 0.05$); unadjusted data presented.
3 Roots < 1 mm diameter.

The analysis of individual treatment regressions indicates that the slope of the regression equation of N content in two-year-old needles versus initial root collar diameter^2 for the rank-plus-N treatment had a negative slope and all other treatments showed positive slopes (Appendix 5.5b). However, the regression was not significant for this treatment and interpretation is unreliable and unadjusted data are presented.

The N content of aboveground tree components showed no significant interaction ($P < 0.05$) between the level of competing vegetation and added N. However, this interaction was significant ($P = 0.0586$) for total belowground N content of trees (Fig. 5.5). Significant responses to added N occurred mainly in current tissues e.g. needles, and stem wood and root systems. Total tree N content was significantly increased by the addition of N ($P = 0.0808$). This was the result of increases in N content of stem wood and the root system of 47 and 22%, respectively. The addition of N also increased current foliage content ($P = 0.0818$) but not total foliage N content.

All tree components, except two-year-old needles, older wood and fine roots, had higher N contents in the spraying treatments compared to in the plus-pasture treatments.

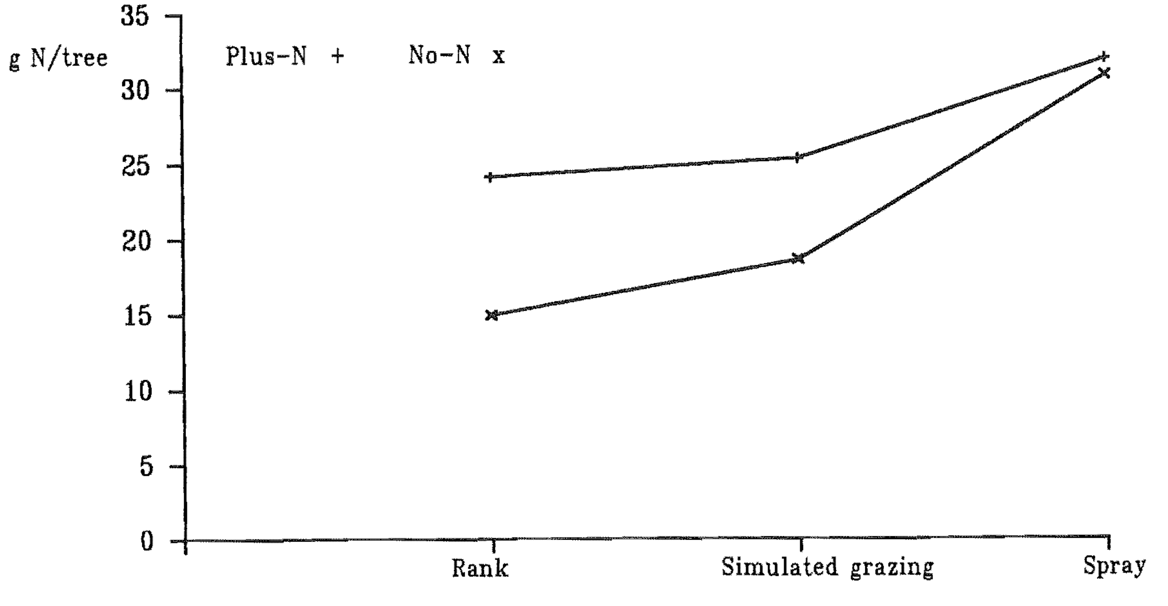


Figure 5.5 Interaction of applied nitrogen and level of competing vegetation on total nitrogen content of belowground biomass of *P. radiata*.

On average, spraying increased total tree N content by 78% (equivalent to 70 kg N/ha) (Table 5.7, Appendix 5.5a), compared to treatments where pasture was present. Some 58% of this response was due to more N being present in the current needle biomass.

5.6 ^{15}N uptake: nitrogen derived from ^{15}N-labelled fertilizer

5.6.1 Proportion of nitrogen derived from ^{15}N-labelled fertilizer in competing vegetation

The seasonal pattern of %Ndff in the pasture in the simulated-grazing treatment was discussed in Section 4.3.1.

There were a few weeds present in the sprayed plots at the end of the experiment. The plots had last been sprayed 137 days after addition of labelled N. The %Ndff for these weeds and for rank pasture are presented in Table 5.8. It is not possible to make meaningful comparisons between treatments.

Table 5.8 %Ndff in competing vegetation in rank and spray treatments.

	Rank	Spray
Replicate	Plus-N	Plus-N
	%	
1	3.818	3.82
2	4.394	2.34
3	4.023	1.65

5.6.2 Proportion of nitrogen derived from ^{15}N-labelled fertilizer in tree biomass components, pasture roots and litter

The seasonal pattern of %Ndff in needles was discussed in Section 4.4.3. For the trees there were no significant differences between treatments at the final harvest (Table 5.9, Appendix 5.6). There are, however, some interesting trends. For nearly all components except current wood, bark and branches, the $^{15}NO_3^-$ had the highest %Ndff. The rank treatment had consistently lowest %Ndff for aboveground components but had higher %Ndff for belowground components than the $^{15}NH_4^+$ simulated-grazing treatments.

Table 5.9 %Ndff in tree biomass components and pasture roots and litter at final harvest.

	Grazing		Rank	Spray			
	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]	P[2]	%Ndff (n = 12)
			%				
Needles[3]							
CNUMC	1.14	0.87	0.81	1.19	0.162	0.3208	1.00
CNUC	1.49	1.03	0.88	1.29	0.216	0.2745	1.17
Y1UC	0.84	0.57	0.45	0.68	0.127	0.1811	0.64
CNLC	1.34	0.98	0.84	1.28	0.209	0.3304	1.11
Y1LC	0.66	0.51	0.40	0.62	0.117	0.4473	0.55
Y2LC	0.46	0.28	0.26	0.51	0.086	0.1862	0.38
Branches							
Current	1.23	0.88	0.78	0.47	0.167	0.2529	1.01
Older	1.02	0.67	0.66	0.92	0.128	0.2022	0.82
Wood							
Current	1.07	0.84	0.69	1.10	0.141	0.2135	0.92
Older	0.70	0.49	0.45	0.49	0.071	0.1350	0.53
Bark							
Current	1.00	0.80	0.67	1.16	0.182	0.3100	0.91
Older	0.89	0.70	0.62	0.96	0.135	0.3229	0.79
Roots							
Fine roots[4]	1.61	1.19	1.54	1.56	0.158	0.2887	1.47
Coarse roots	1.12	0.96	1.03	1.11	0.103	0.6558	1.05
Stump	0.87	0.71	0.75	0.99	0.113	0.3559	0.83
Buds	1.37	0.98	0.98	1.27	0.167	0.2971	1.15
Pasture roots	2.41	2.76	3.16	-	0.544	0.6433	
Litter	1.82	2.17	3.07	1.14	0.113	0.0001	
Treatment means	1.05	0.78	0.74	0.98			

1 Standard error.
2 Probability of treatment differences according to ANOVA.
3 KEY

CNUMC	Current needles uppermost crown
CNUC	Current needles upper crown
Y1UC	One-year-old needles upper crown
CNLC	Current needles lower crown
Y1LC	One-year-old needles lower crown
Y2LC	Two-year-old needles lower crown

4 Roots < 1 mm diameter.

There were no significant differences in %Ndff in pasture roots (Appendix 5.6) although the %Ndff in litter was highest in the rank plots with the %Ndff significantly greater in the rank plots than in either the simulated-grazing or sprayed treatments (Appendix 5.6).

A split plot design was used to examine the differences in %Ndff between tree biomass components (Appendix 5.7) using trees as main plots and components as subplots. The main treatment effects were not significant at $P < 0.05$. Scheffes test was used to examine differences between components (Table 5.9, Appendix 5.8).

The %Ndff was highest in pine roots less than 1 mm diameter (Table 5.9) where it was significantly higher than in all other tree biomass components ($P < 0.05$) (Appendix 5.8).

The %Ndff was significantly lower in two-year-old needles in the lower crown compared with all components except one-year-old needles and older wood. There were no significant differences in %Ndff among current needles and other current tissues (wood, bark, and branches) and coarse roots.

Removal of pasture competition significantly increased average %Ndff for all components by 29% compared to the plus-pasture treatments ($P = 0.0001$) and %Ndff was significantly higher in $^{15}NO_3^-$-treated than $^{15}NH_4^+$-treated trees ($P = 0.0001$); this was equal to an increase of 35% (Appendix 5.7).

5.7 ^{15}N uptake and ^{15}N recovery in tree and pasture components

5.7.1 ^{15}N uptake by competing vegetation

The seasonal pattern of fertilizer uptake by pasture in the simulated-grazing treatment was discussed in Section 4.3.2.

Pasture management had a significant ($P < 0.001$) effect on recovery of ^{15}N in aboveground pasture herbage (Table 5.10, Appendix 5.9), with the recovery of ^{15}N in rank herbage being one quarter and one sixth the value in $^{15}NH^+{}_4$-treated and $^{15}NO_3^-$-treated simulated-grazing treatments, respectively. In the simulated-grazing treatment, ^{15}N recovery in aboveground pasture herbage for the $^{15}NO_3^-$-treated treatment was 40% greater than in the $^{15}NH_4^+$ treatment.

There were no significant differences between treatments in ^{15}N recovery in the belowground biomass to a depth of 20 cm. Moreover, ^{15}N recovery was not assessed for any biomass components below this depth.

Table 5.10 **Percent ^{15}N recovery in competing vegetation.**

	Grazing		Rank	
	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
		%		
Aboveground	42.48	30.38	7.52	2.695
Roots	2.94	6.21	8.03	3.321
Total	45.42	36.59	15.55	5.235

1 Standard error.

There were no significant differences in total ^{15}N recovery in the simulated-grazing treatment between the different forms of labelled N (Table 5.10). This was due to the higher recovery of $^{15}NH_4^+$ in root biomass.

Total ^{15}N recovery in the rank plots was significantly lower than in the simulated-grazing treatments even though more than 50% of ^{15}N was recovered in root biomass.

5.7.2 ^{15}N uptake and recovery by *P. radiata*

There were significant differences ($P < 0.05$) in ^{15}N recovery between treatments (Appendices 5.10a and 5.10b). Thus, the recovery of ^{15}N in current needles and branches was significantly lower in treatments with competing vegetation than in the sprayed treatment.

The recovery of ^{15}N in some tree biomass components shown in Table 5.11 was corrected for initial tree size using initial root collar diameter^2 (Appendix 5.11). Although this covariate did not always improve the statistical analysis it was used for all components to maintain consistency.

There were several cases where the use of initial root collar diameter^2 as a covariate for recovery in the various biomass components suggested significantly different ($P < 0.05$) regression slopes for the treatments. However, for ^{15}N recovery in older branches and fine roots some of the individual regressions were poor suggesting that initial root collar diameter^2 was not a suitable covariate.

Examination of individual treatment regressions of older wood against initial root collar diameter^2 showed that all regressions were not significant ($P < 0.05$), except for the rank treatment. For all treatments except $^{15}NO_3^-$ in the simulated-grazing treatments the slope of the regression equation was positive (Fig. 5.6). However, given that this regression was not significant for the $^{15}NO_3^-$ simulated-grazing treatment, no obvious explanation can be offered to explain this observation, and data were not adjusted for the covariate (Appendix 5.10a).

Recovery of ^{15}N in aboveground tree components was significantly higher ($P = 0.0374$) in the sprayed treatment and contained more than twice the ^{15}N than in plots with competing pasture (Table 5.11, Appendix 5.11). In contrast, there was no difference in ^{15}N uptake by belowground components between treatments, however, total ^{15}N recovery by *P. radiata* was still significantly higher in the sprayed treatment (Table 5.11, Appendix 5.11). Total tree recovery was 115% higher in the no-pasture treatment than in the plus-pasture treatment.

Although there were no statistically significant differences ($P < 0.05$) between rank and simulated-grazing treatments, ^{15}N recovery was somewhat lower in the rank treatment than in the simulated-grazing treatment. Furthermore, the differences between recovery of $^{15}NO_3^-$ and $^{15}NH_4^+$ were not statistically significant although recovery was slightly higher for $^{15}NO_3^-$ (Table 5.11, Appendix 5.11).

The removal of pasture competition resulted in significantly higher ^{15}N recovery in current needles and branches ($P < 0.05$) and also in current buds ($P = 0.0771$). This treatment also significantly ($P = 0.0022$) increased ^{15}N recovery in needle biomass. There were no other significant treatment effects (Appendix 5.11).

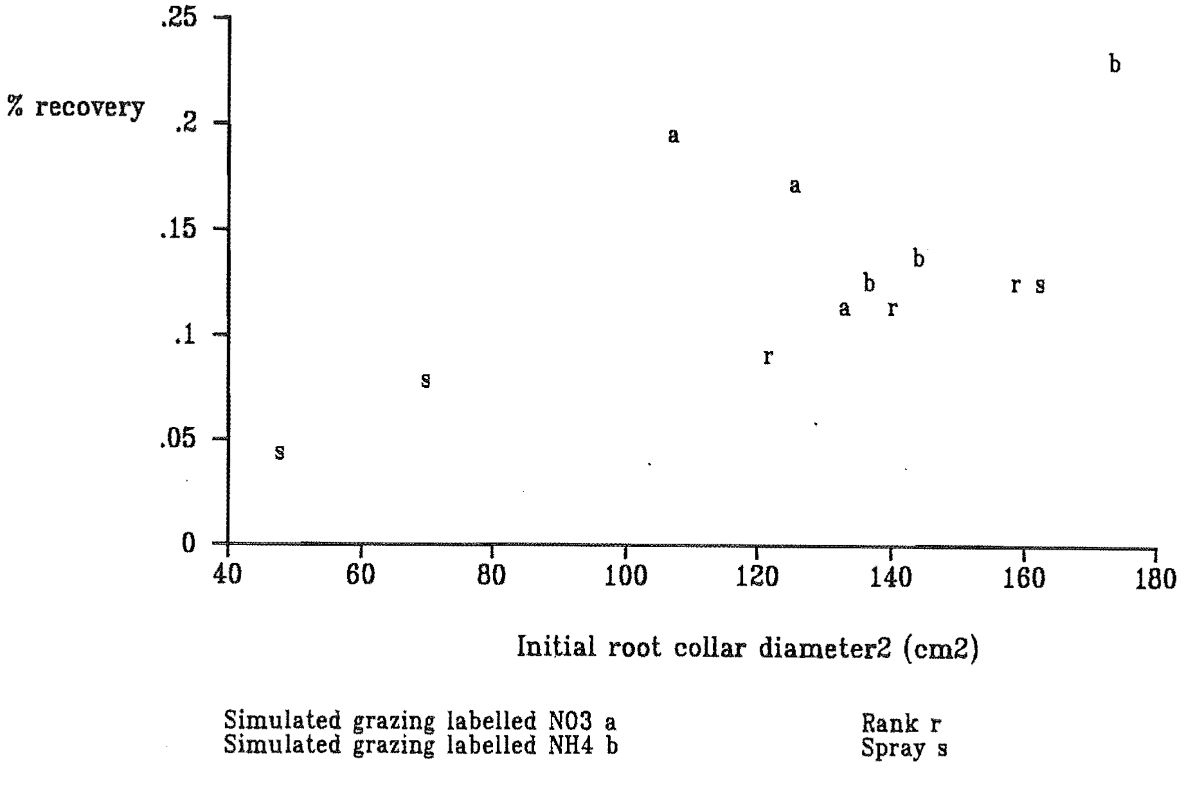


Figure 5.6 Interaction between treatment and ^{15}N recovery in old wood.

Table 5.11 Percent ^{15}N recovery in biomass components adjusted for initial tree size effects where appropriate.

Tree components	Grazing		Rank	Spray	S.E.[1]	P[2]
	Plus-N $^{15}NO_3^-$	Plus-N $^{15}NH_4^+$	Plus-N $^{15}NH_4^+$	Plus-N $^{15}NH_4^+$		
			%			
Foliage						
Current	5.2	3.6	3.1	9.4	0.65	0.0060
1-year-old	1.2	1.3	0.6	1.4	0.23	0.2100
2-year-old[3]	0.2	0.2	0.1	0.1	0.05	0.5443
Total	6.6	4.9	3.8	10.9	0.89	0.0205
Branches						
Current	0.5	0.5	0.4	0.9	0.08	0.0733
Older[3]	0.7	0.8	0.6	0.9	0.17	0.6623
Stem						
Current	0.5	0.5	0.2	0.7	0.11	0.2272
Older[3]	0.2	0.2	0.1	0.1	0.02	0.1050
Bark						
Current	0.04	0.04	0.01	0.05	0.012	0.5414
Older	0.3	0.3	0.1	0.4	0.18	0.1649
Buds	0.1	0.2	0.1	0.4	0.08	0.2302
Total aboveground	9.0	7.2	5.3	14.3	1.28	0.0374
Roots						
Fine[3,4]	0.1	0.2	0.1	0.1	0.03	0.6477
Coarse	0.3	0.4	0.5	0.6	0.06	0.1758
Stump	0.3	0.3	0.3	0.4	0.05	0.6339
Total belowground	0.8	0.9	0.9	1.1	0.12	0.5083
Total tree	9.8	8.1	6.2	15.4	1.37	0.0463

1 Standard error.
2 Probability of treatment differences according to ANCOVA.
3 Non-parallel lines, $P < 0.05$, unadjusted means presented.
4 Roots < 1 mm diameter.

5.7.3 Effect of simulated-grazing on *P. radiata* ^{15}N uptake

The interpretation of the experimental grazing treatment needs to take into account that the ^{15}N removed in successive pasture harvests was not returned to the plots; unlabelled N was used instead. This diluted the ^{15}N pool in the soil. If ^{15}N had been used in the returned component then recovery of ^{15}N by trees in the simulated-grazing treatment may have been somewhat higher, as would have been ^{15}N recovery by the pasture component.

Undoubtedly ^{15}N recovery was reduced in the plus-pasture treatments by the presence of pasture. Recalculation of recovery by the tree, assuming that the total ^{15}N applied was reduced by the amount of ^{15}N removed in clipped pasture or retained by rank pasture, showed that although tree recovery was greatest in the $^{15}NO_3^-$-treated plots and least in the rank treatment there were no significant differences between treatments (Table 5.12, Appendix 5.12a).

Table 5.12 Percent ^{15}N recovery by trees adjusted for ^{15}N removal in clipped pasture or retained in rank pasture.

Grazing		Rank	Spray	
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
	%[2]			
16.98	11.90	6.61	15.77	2.555

1 Standard error.
2 Adjusted for initial differences in tree size using initial root collar diameter^2.

It is possible that the removal of the equivalent of 303 kg N/ha and return of only 29% of this in the simulated-grazing treatment reduced the available N pool and this, combined with the dilution effect, may have also reduced ^{15}N recovery by *P. radiata* in the simulated-grazing-plus-N treatment.

5.7.4 ^{15}N recovery in the litter component

The recovery of ^{15}N in litter was significantly lower ($P = 0.0069$) in the sprayed plots compared with other treatments and ^{15}N recovery was significantly higher in the rank treatment compared with the simulated-grazing treatment. There was no difference between the $^{15}NH_4^+$ and $^{15}NO_3^-$ forms of N (Table 5.13, Appendix 5.13). However, the significantly lower recovery of ^{15}N in the simulated-grazing compared with the rank treatment was probably due to the non-replacement of the ^{15}N removed in the clippings of the pasture treatment.

Table 5.13 Percent ^{15}N recovery in the litter component.

Grazing		Rank	Spray		
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]	P[2]
		%			
2.25	2.65	5.56	1.61	0.565	0.0050

1 Standard error.
2 Probability of treatment differences according to ANOVA.

Recovery in litter in rank plots represented 7.4% of total ^{15}N recovery and 20% of total ^{15}N recovery, excluding recovery in soil.

Adjusting ^{15}N recovery in litter for removal in clipped pasture or retention by rank pasture resulted in there being no significant difference in the quantity of ^{15}N removed between the simulated-grazing and rank treatments ($P = 0.0650$) (Table 5.14, Appendix 5.12b).

Table 5.14 Percent ^{15}N recovery in litter adjusted for ^{15}N removal in clipped pasture or retained in rank pasture.

Grazing		Rank	Sprayed	
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
		%		
3.94	3.84	5.97	1.62	0.706

1 Standard error.

The difference between the rank and the sprayed treatments suggests a major difference in the cycling of ^{15}N between these treatments. In the rank plots, litter provided an important pool of ^{15}N-labelled fertilizer for future plant uptake. This contrasts with the sprayed plots where the litter pool was small compared with future tree demands and the soil pool was a relatively more important source of ^{15}N .

5.8 Summary

- Removal of competition between pasture and trees significantly increased N content of current needles (Section 5.4).

- Removal of pasture increased total tree N content by 70 kg N/ha.

- Pasture in the simulated-grazing treatment recovered a greater amount of ^{15}N-labelled fertilizer than pasture in the rank treatment.

- Similar amounts of $^{15}NO_3^-$ and $^{15}NH_4^+$ were recovered in total pasture biomass, however, more $^{15}NO_3^-$ than $^{15}NH_4^+$ was removed in clipped pasture.

- The ability of *P. radiata* to utilize ^{15}N-labelled fertilizer applied on one occasion during a program of split fertilizer applications was severely limited by the presence of competing pasture.

- *P. radiata* assimilated the same amount of ^{15}N when added as $^{15}NO_3^-$ or NH_4^+.

- Litter on rank plots may be an important source of ^{15}N for future plant uptake.

Chapter Six

System recovery of ^{15}N

6.1 Introduction

In earlier chapters the dynamics and recovery of ^{15}N in various ecosystem components was reported; in this chapter a final budget of ^{15}N recovery by trees and competing vegetation and in soils to a depth of 20 cm is presented. An understanding of the effect of competing vegetation on the distribution of ^{15}N in the system and on total ^{15}N recovery enables further evaluation of the competition between trees and pasture.

6.2 Retention of ^{15}N in soils and recovery of ^{15}N from the 0-10 and 10-20 cm soil depths

Recovery of ^{15}N in the final collection of soil samples from the sprayed treatment indicated a considerable loss of ^{15}N (Section 4.2.2). Decaying pasture roots had been removed during the sieving of soils and this was thought to be the likely cause. Therefore, for these samples only, the decayed roots were returned to sieved soils prior to grinding and analysis.

^{15}N retained in the soil was assessed 249 days after ^{15}N application. There were no significant differences ($P < 0.05$) between treatments in the proportion of N derived from ^{15}N-labelled fertilizer (%Ndff) (Table 6.1, Appendix 6.1a) in either the 0-10 or 10-20 cm soil depths. The %Ndff decreased rapidly down the profile (Table 6.1) - %Ndff in the 10-20 cm soil depth was only 28% of that in the 0-10 cm soil depth when data for $^{15}NO_3^-$- and $^{15}NH_4^+$-treated simulated-grazing and rank and sprayed treatments were averaged.

In the 20-60 cm soil depth, %Ndff was not statistically analyzed because some samples were apparently ^{15}N-depleted and replication was poor (Appendix 6.2).

There were no significant differences ($P < 0.05$) between treatments in the recovery of ^{15}N in either the 0-10 or 10-20 cm soil depths (Table 6.2, Appendix 6.1b). The average recovery of ^{15}N in the 10-20 cm for all treatments is only 20% of the average recovery in the 0-10 cm soil depth. This suggests that there was very little leaching of ^{15}N below 10 cm as a result of the low rainfall during the period 15 September to 29 April (215 mm). The condition of low soil moisture was also enhanced by the dry winter prior to ^{15}N addition. Furthermore, the analyses of the 20-60 cm samples do not show elevated levels (Appendix 6.2).

Table 6.1 **%Ndff in total soil nitrogen in the 0-10 and 10-20 cm soil depths 249 days after ^{15}N-labelled fertilizer application.**

	Simulated-grazing		Rank	Spray	
Soil depth (cm)	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
			%		
0-10	0.370	0.373	0.400	0.462	0.0721
10-20	0.111	0.096	0.126	0.115	0.0283

1 Standard error.

The analysis of variance for ^{15}N recovery in the 0-20 cm soil depth shows that there were no significant differences between treatments (Table 6.2, Appendix 6.1b). On average 49% of ^{15}N applied in spring was recovered in the 0-20 cm soil depth. The inclusion of decaying pasture roots in the soil sample for the sprayed plots increased recovery on average by 8.4%.

Table 6.2 **Percent ^{15}N recovery in 0-10 and 10-20 cm soil depths 249 days after ^{15}N-labelled fertilizer application.**

	Simulated-grazing		Rank	Spray	
Soil depth (cm)	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
			%		
0-10	40.8	35.6	40.4	47.3	8.00
10-20	8.7	7.2	9.0	8.4	2.03
0-20	49.6	42.9	47.8	55.7	8.67

1 Standard error.

6.3 Total system recovery of ^{15}N

^{15}N recovery in trees, competing vegetation, litter and soils to a depth of 20 cm (Appendix 6.3) was summed for each plot (Table 6.3a) and an analysis of variance was performed on total system ^{15}N recovery. The significant treatment difference (Appendix 6.3) was due to the high recovery in the $^{15}NO_3^-$-treated simulated-grazing treatment and the low recovery in the other treatments, especially the low recovery in the rank and spray treatments. This difference in system recovery is probably due to the high recovery of ^{15}N in pasture in the

Table 6.3a **Total system (trees, pasture, litter and soils to a depth of 20 cm) recovery of ^{15}N 249 days after application in spring 1988.**

Simulated-grazing		Rank	Spray	
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
		%		
106.6	91.6	75.8	71.0	6.35

[1] Standard error.

$^{15}NO_3^-$-treated plots compared with the other treatments (Table 6.3b). There were no other significant treatment differences.

The use of analysis of covariance did not improve the analysis (Appendix 6.4). Removal of pasture competition reduced system ^{15}N recovery by 22% compared with the rank and simulated-grazing treatments. The simulated-grazing treatment increased system ^{15}N recovery by 31% compared to the rank treatment and the form of labelled N did not affect system ^{15}N recovery ($P < 0.1$) (Appendix 6.5).

On average, 86% of the single labelled split application was recovered in the combined tree and pasture biomass and soils to a depth of 20 cm in a 1.9-m-radius unconfined plot. The ^{15}N that cannot be accounted for was 4.1 kg N/ha (14% of the ^{15}N applied).

The average recovery of ^{15}N in the 20-60 cm for all treatments was 3.81% (standard deviation = 1.71%). When the ^{15}N recovered in trees, pasture, litter and soils (Table 6.3a) is adjusted for the average amount of ^{15}N recovered in the 20-60 cm soil depth (3.81%), the amount of ^{15}N unaccounted for is reduced to approximately 10%.

Although there was no difference in total system recovery between the $^{15}NH_4^+$-treated treatments there were highly significant differences between treatments in the quantity of ^{15}N recovered in the combined above and belowground biomass components of trees and pasture (Table 6.4, Appendix 6.6).

On average, more than twice as much ^{15}N was recovered in the combined above and belowground biomass components in treatments with pasture than in the sprayed treatment. As well, the simulated-grazing treatment significantly increased ^{15}N recovery by vegetation by 106% compared with the rank treatment. However, there was no significant difference between recovery of $^{15}NH_4^+$ and $^{15}NO_3^-$ in the simulated-grazing experiment.

Table 6.3b Percent ^{15}N recovery in major ecosystem components.

	Grazing		Rank	Spray
	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$
		%		
Tree				
Aboveground	9.0	7.2	5.3	14.3
Belowground	0.8	0.9	0.9	1.1
Total tree	**9.8**	**8.1**	**6.2**	**15.4**
Pasture				
Aboveground	42.5	30.4	7.5	0.2
Belowground	2.9	6.2	8.0	-
Total pasture	**45.4**	**36.6**	**15.5**	**0.2**
Litter	2.2	2.7	5.6	1.6
Soil 0-10 cm				
Inorganic	21.8	13.8	13.0	14.1
Organic	19.0	21.8	27.4	33.2
Soil 10 -20 cm				
Organic	8.7	7.2	9.0	8.4
Total soil 0-20 cm	**49.5**	**42.8**	**49.4**	**55.7**

Table 6.4 Percent ^{15}N recovery in combined above and belowground biomass components of trees and pasture 249 days after ^{15}N application.

Simulated-grazing		Rank	Spray	
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
		%		
54.85	46.10	24.49	13.73	4.364

1 Standard error.

To account for losses from the unconfined ^{15}N-treated plots that may have occurred, current needles in the upper crown of trees surrounding the ^{15}N-treated tree were collected just after the harvest of all trees was completed. On average, less than 0.25% of the total quantity of ^{15}N-labelled fertilizer applied was recovered in surrounding trees with no differences between treatments (Table 6.5, Appendix 6.7).

Table 6.5 Percent ^{15}N recovered in trees surrounding the unconfined ^{15}N-treated plots.

Simulated-grazing		Rank	Spray	
$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$	S.E.[1]
		%		
0.206	0.173	0.287	0.297	0.1389

1 Standard error.

Unidentified fungal fruiting bodies were collected at the end of the experiment from $^{15}NH_4^+$-treated simulated-grazing and sprayed treatments and their N contents were analyzed (Appendix 6.8). The %Ndff was 16 times higher in the simulated-grazing treatment than in the sprayed treatment. It is not possible to interpret the role of the fungal biomass in system ^{15}N recovery as there were no observations made of fungal biomass.

6.4 Summary

- Pasture competition did not affect the recovery of ^{15}N in the 0-10 cm depth of soil.

- ^{15}N recovery in the combined above and belowground biomass in the simulated-grazing treatment was more than three times as great as in the sprayed treatment and more than twice as great as in the rank treatment.

- Total system recovery of $^{15}NH_4^+$ was similar for all treatments and on average up to 90% of the ^{15}N-labelled fertilizer applied in spring was recovered 249 days after application.

- On average, losses from one ^{15}N-labelled application of 30 kg N/ha applied in spring as part of a program of split N fertilizer applications were low, approximately 10%.

- Leaching did not appear to be an important mechanism for loss of applied ^{15}N.

Chapter Seven

Nitrogen supply

7.1 Introduction

Data were collected at monthly intervals from *in situ* soil incubations to estimate seasonal dynamics of soil mineral N, net N mineralization, nitrification and N uptake by vegetation, and to identify the predominant form of mineral N taken up by trees in the six treatments. Such an approach has been successfully used by Nadelhoffer *et al.* (1984, 1985), Dyck *et al.* (1987), Smethurst and Nambiar (1989), and Raison *et al.* (1990).

7.2 Concentration of soil mineral nitrogen

Ambient mineral N concentrations were determined both at the start and the end of *in situ* incubations between 21 April 1988 and 27 April 1989. The seasonal pattern of mineral N (NH_4^+-N and NO_3^--N) was analyzed using repeated measures analysis of variance for both 0-5 cm and 5-15 cm soil depths (Appendix 7.1).

The interaction of time x level of pasture competition x monthly addition of N was significant ($P < 0.05$) for the 0-5 cm soil depth. The dynamics of mineral N production during the experiment in the 0-5 cm soil depth were complicated but some trends were apparent (Fig. 7.1). For example, in the rank-no-N treatment mineral N concentration peaked in January 1989 at 49 μg/g and by April 1989 it was back to a level similar to that of April 1988. In all other treatments soil mineral N concentrations increased during the experiment; the differences between those treatments receiving monthly additions of N and those that did not increased with time (Fig. 7.1).

The increase in soil mineral N concentration during the experiment was expected because all treatments, except rank-no-N and spray-no-N, received N as returns in clippings removed or as monthly additions of N. In the spray-no-N treatment mineral N levels increased due to reduced plant uptake and presumably the release of N from decaying pasture and pasture roots.

There was no significant interaction between time x level of pasture competition x monthly addition of N in the 5-15 cm soil depth ($P > 0.05$) (Fig. 7.2a, Appendix 7.1), although the individual treatment (level of pasture competition and monthly addition of N) interactions with time were both significant ($P<0.05$) (Figures 7.2b and 7.2c). Ambient mineral N concentrations in the 5-15 cm soil depth increased during the experiment with the difference between the

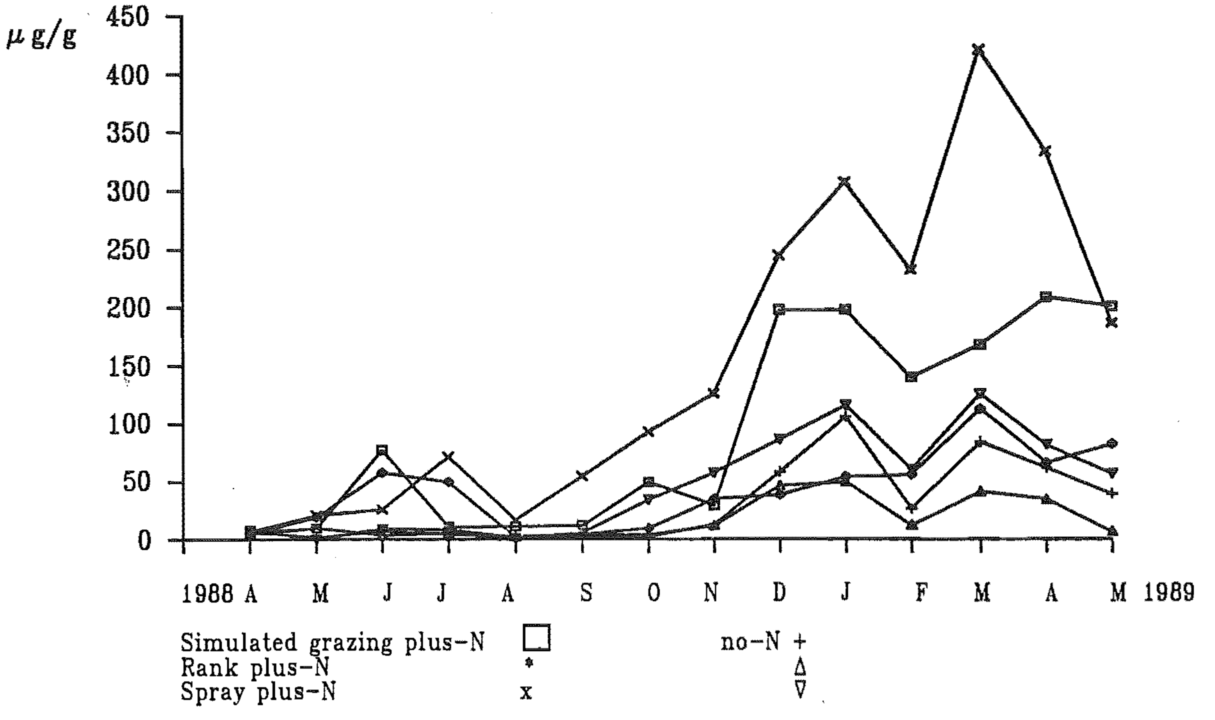


Figure 7.1 **Mineral nitrogen (NH_4^+ + NO_3^-) concentrations in the 0-5 cm soil depth, April 1988-May 1989.**

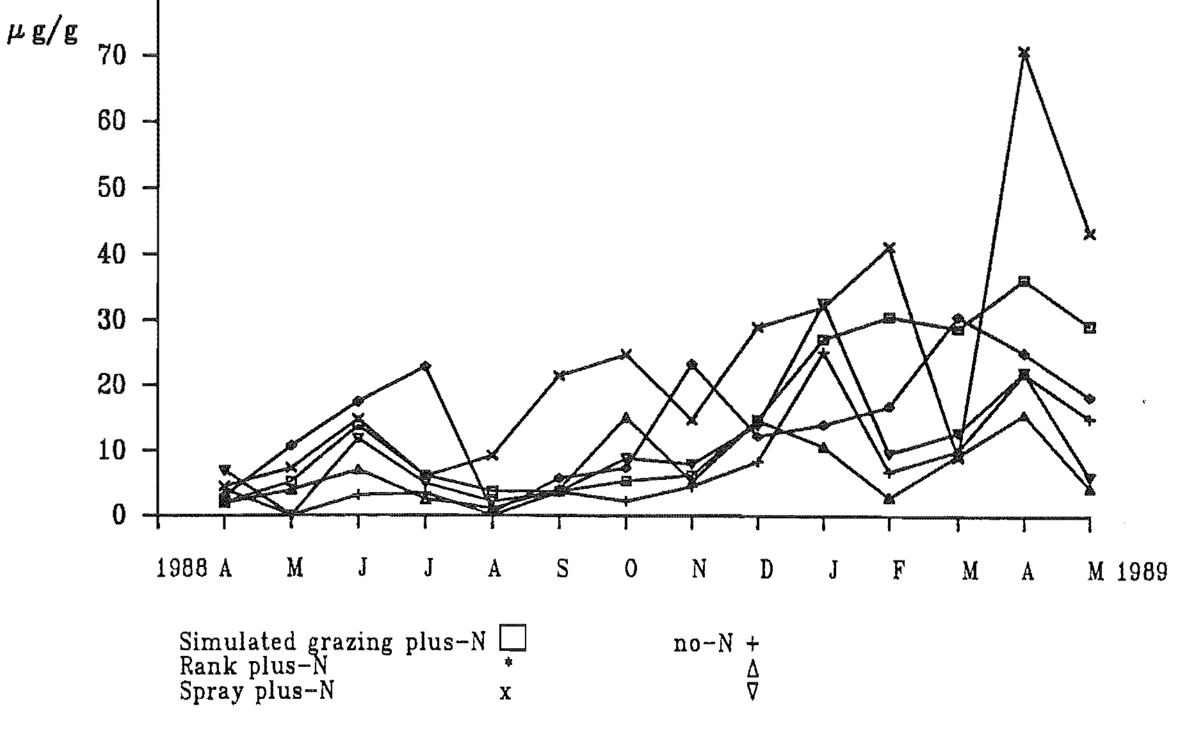


Figure 7.2a **Mineral nitrogen (NH_4^+ + NO_3^-) concentrations in the 5-15 cm soil depth, April 1988-May 1989.**

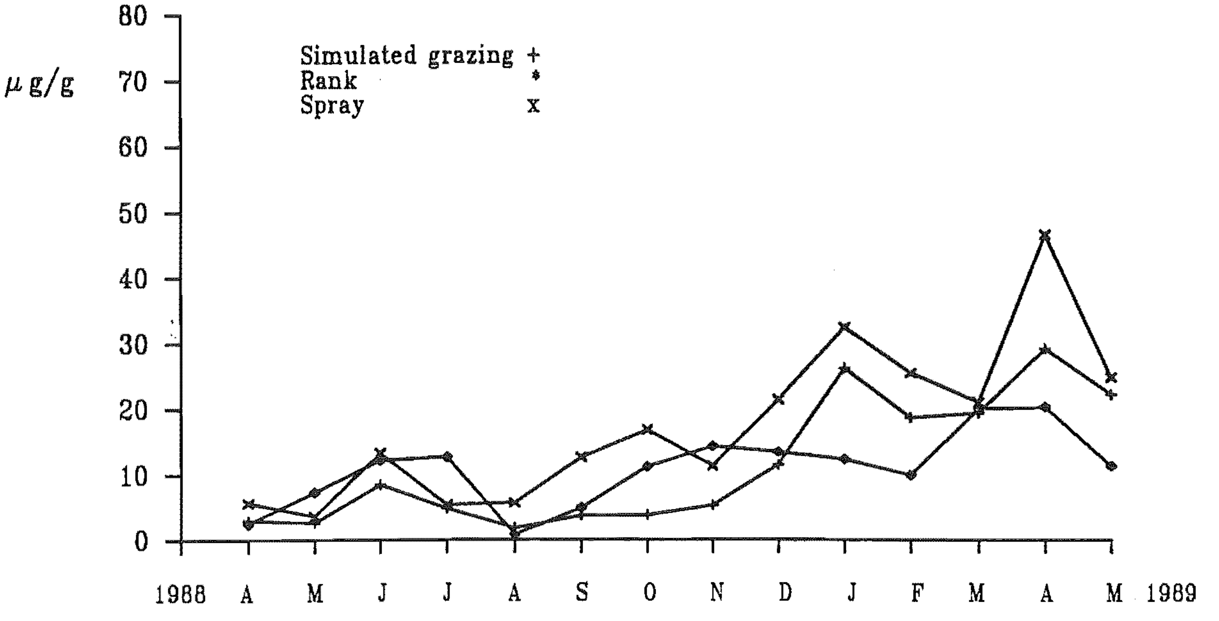


Figure 7.2b Mineral nitrogen (NH_4^+ + NO_3^-) concentrations in the 5-15 cm soil depth as influenced by level of pasture competition, April 1988-May 1989.

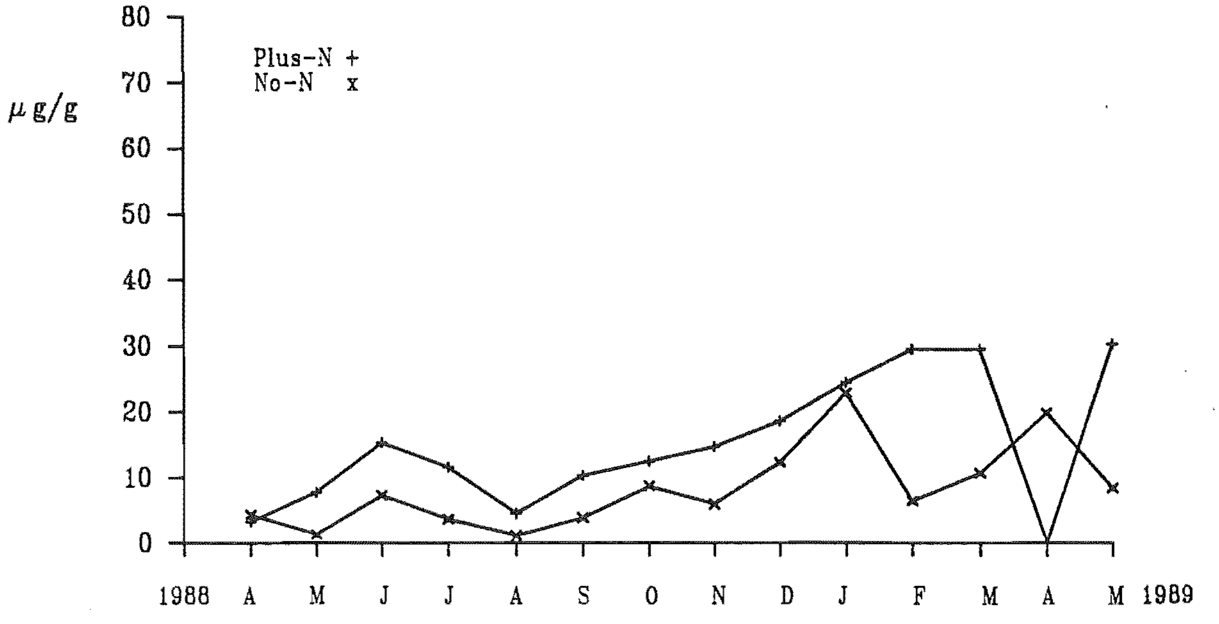


Figure 7.2c Mineral nitrogen (NH_4^+ + NO_3^-) concentrations in the 5-15 cm soil depth as influenced by the monthly addition of nitrogen, April 1988-May 1989.

treatments increasing with time, especially between the sprayed and rank treatments (Fig. 7.2b).

Ambient mineral N concentrations in the 5-15 cm soil depth increased immediately after the first addition of N in April 1988 (Fig. 7.2c) and continued to do so except at the August 1988 and April 1989 samplings when ambient mineral N concentrations in the plus-N treatments decreased from the previous sampling. Although there were seasonal fluctuations in ambient mineral N concentrations in the no-N treatment, the April 1989 sampling showed only a small increase over the April 1988 sampling.

There was a significant interaction between the level of pasture competition and distance from the stem for ambient mineral N concentration in the 0-5 cm soil depth ($P<0.05$) (Appendix 7.1).

In the 0-5 cm soil depth, at both distances from the stem, the sprayed treatments had the highest concentration of mineral N and mineral N concentration was nearly always higher between 1 and 2.5 m radius from the stem than within a 1 m radius of the stem (Figures 7.3a and 7.3b). Mineral N was always lowest in the rank treatments. The same pattern also occurred in the 5-15 cm soil depth (Figures 7.4a and 7.4b), but was only significant at $P<0.1$.

7.3 Net nitrogen mineralization

Net N mineralization in the field soils was estimated using the *in situ* buried polyethylene bag method (Westermann and Crothers, 1980; Nadelhoffer *et al.*, 1984). This method assumes that the gaseous loss of N relative to N mineralization is negligible, that there can be no leaching or root uptake of N from the plastic bag, and that the conditions in the plastic bag do not interfere with N transformations.

Nadelhoffer *et al.* (1984) defined net ammonification and nitrification in incubations as:

7.1 Ammonification; $\Delta\, NH_4^+\text{-}N = NH_4^+\text{-}N_{a(t+1)} - NH_4^+\text{-}N_{i(t)}$

7.2 Nitrification; $\Delta\, NO_3^-\text{-}N = NO_3^-\text{-}N_{a(t+1)} - NO_3^-\text{-}N_{i(t)}$

where

$NH_4^+\text{-}N_{i(t)}$	=	mean NH_4^+-N content of initial, non-incubated soil samples at the start of interval t.
$NH_4^+\text{-}N_{a(t+1)}$	=	mean NH_4^+-N content accumulated incubated soil samples at the end of interval t.
$\Delta\, NH_4^+\text{-}N$	=	net ammonification in incubations.
$NO_3^-\text{-}N_{i(t)}$	=	mean NO_3^--N content of initial, non-incubated soil samples at the start of interval t.
$NO_3^-\text{-}N_{a(t+1)}$	=	mean NO_3^--N content accumulated in incubated soil samples at the end of interval t.
$\Delta\, NO_3^-\text{-}N$	=	net nitrification in incubations.

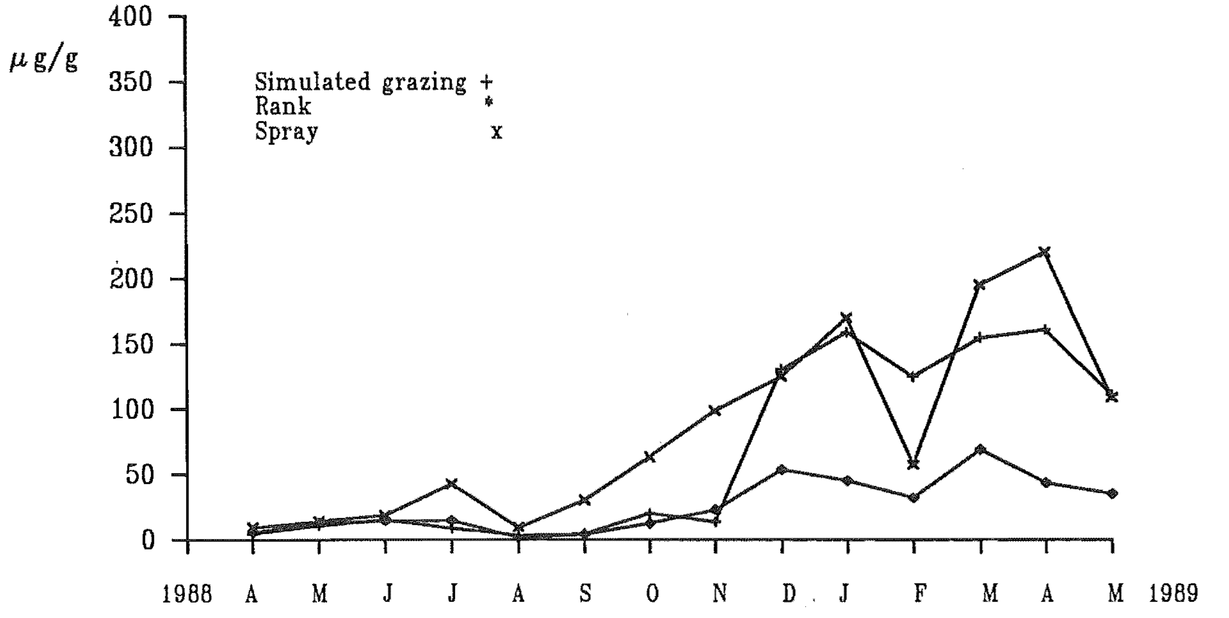


Figure 7.3a Mineral nitrogen ($NH_4^+ + NO_3^-$) concentrations in the 0-5 cm soil depth within 1 m radius of the stem, April 1988-May 1989.

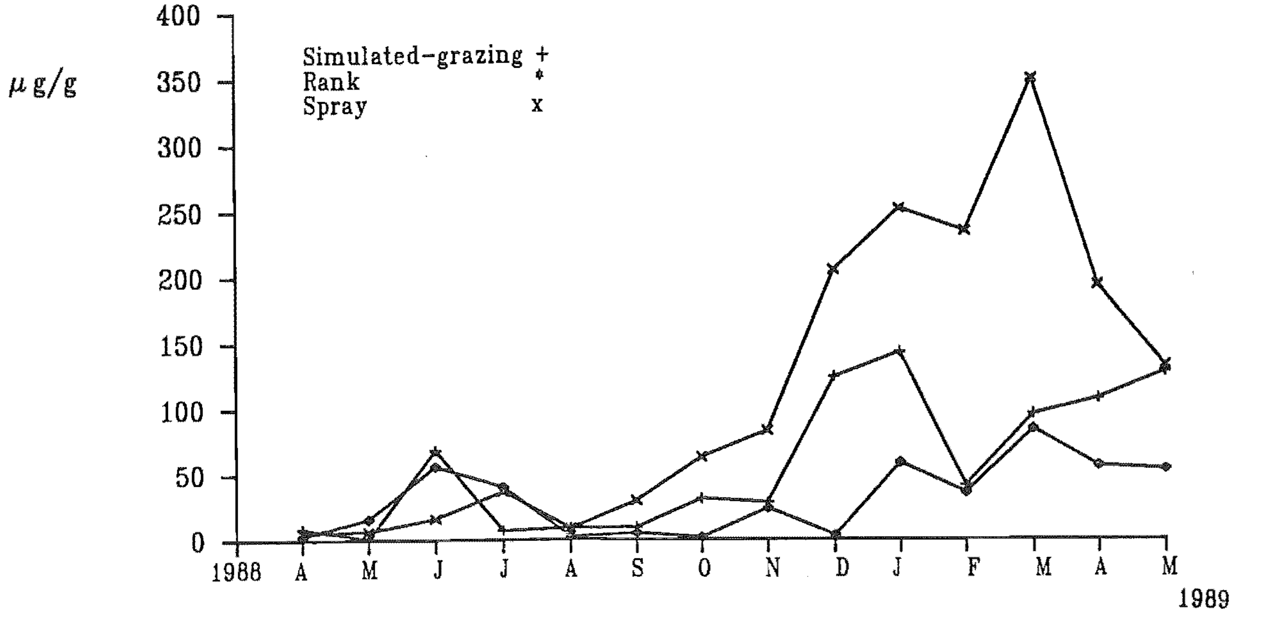


Figure 7.3b Mineral nitrogen ($NH_4^+ + NO_3^-$) concentrations in the 0-5 cm soil depth between 1 and 2.5 m radius of the stem, April 1988-May 1989.

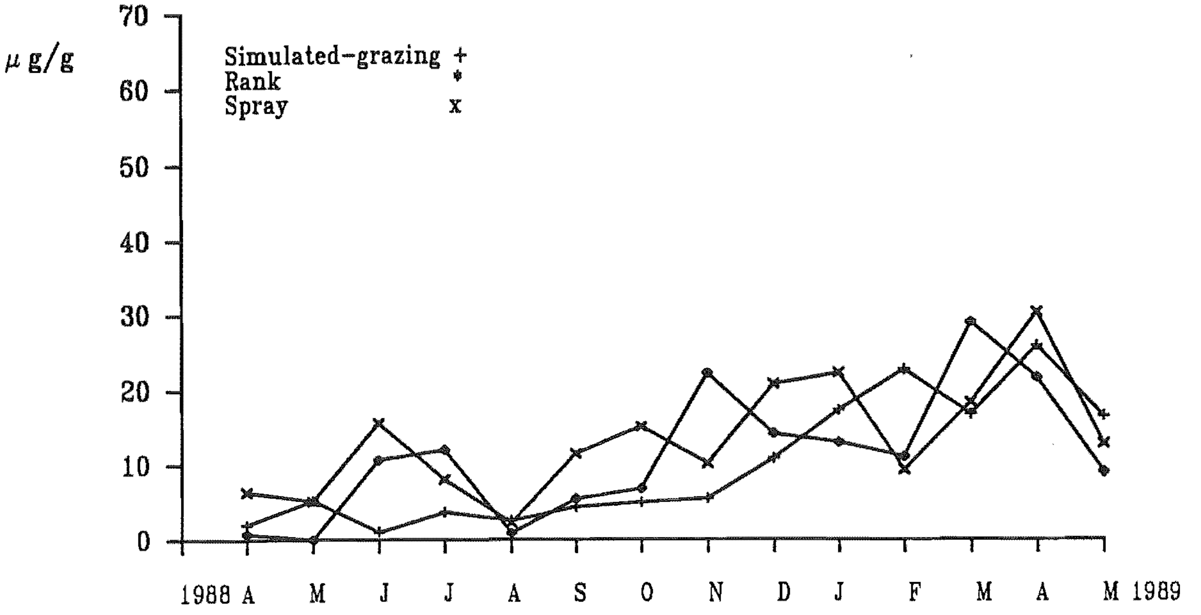


Figure 7.4a **Mineral nitrogen (NH_4^+ + NO_3^-) concentrations in the 5-15 cm soil depth within 1 m radius of the stem, April 1988-May 1989.**

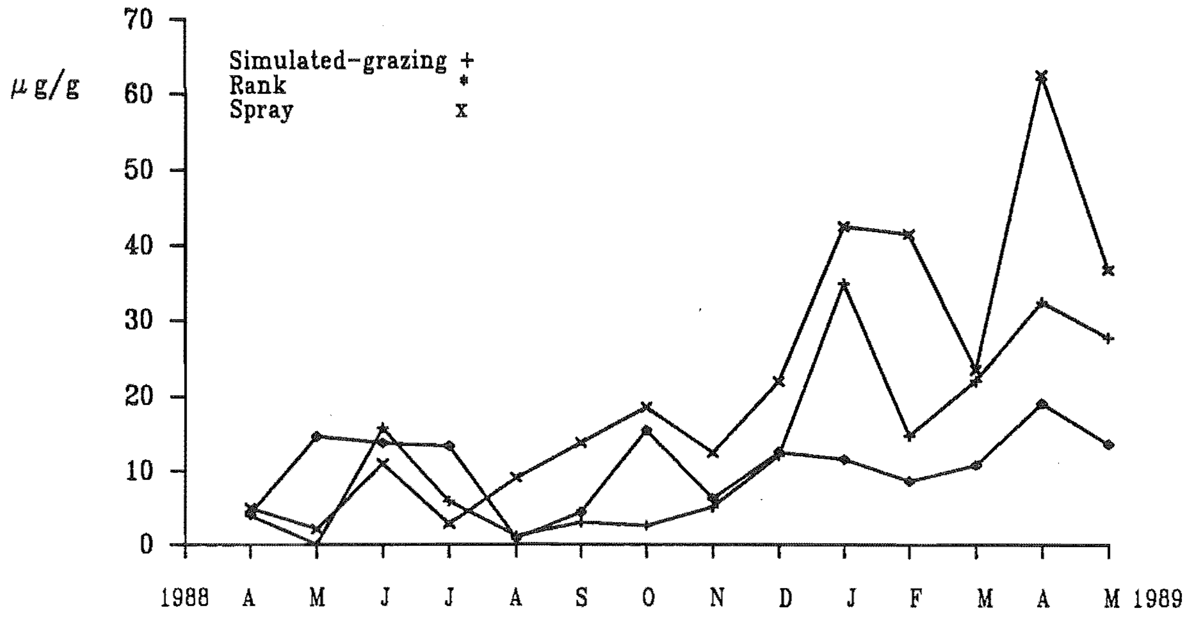


Figure 7.4b **Mineral nitrogen (NH_4^+ + NO_3^-) concentrations in the 5-15 cm soil depth between 1 and 2.5 m radius of the stem, April 1988-May 1989.**

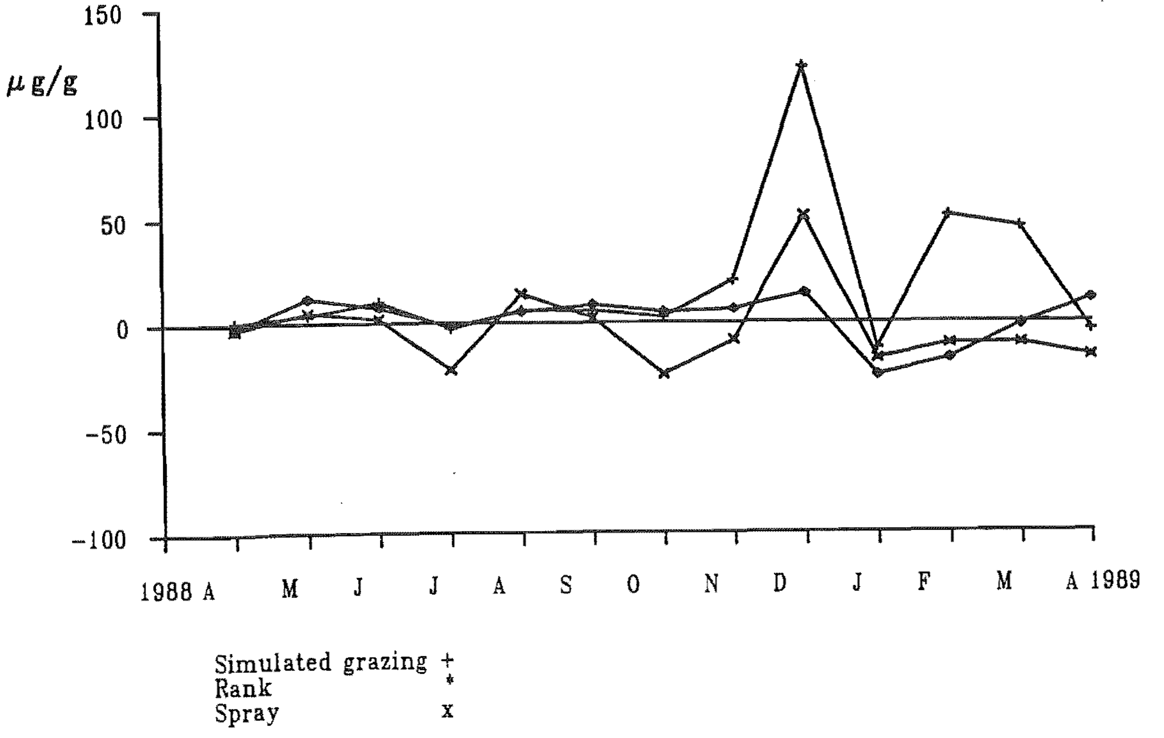


Figure 7.5a Change in NH_4^+-N concentrations in the 0-5 cm soil depth within 1 m radius of the stem as influenced by level of competing vegetation, April 1988-May 1989.

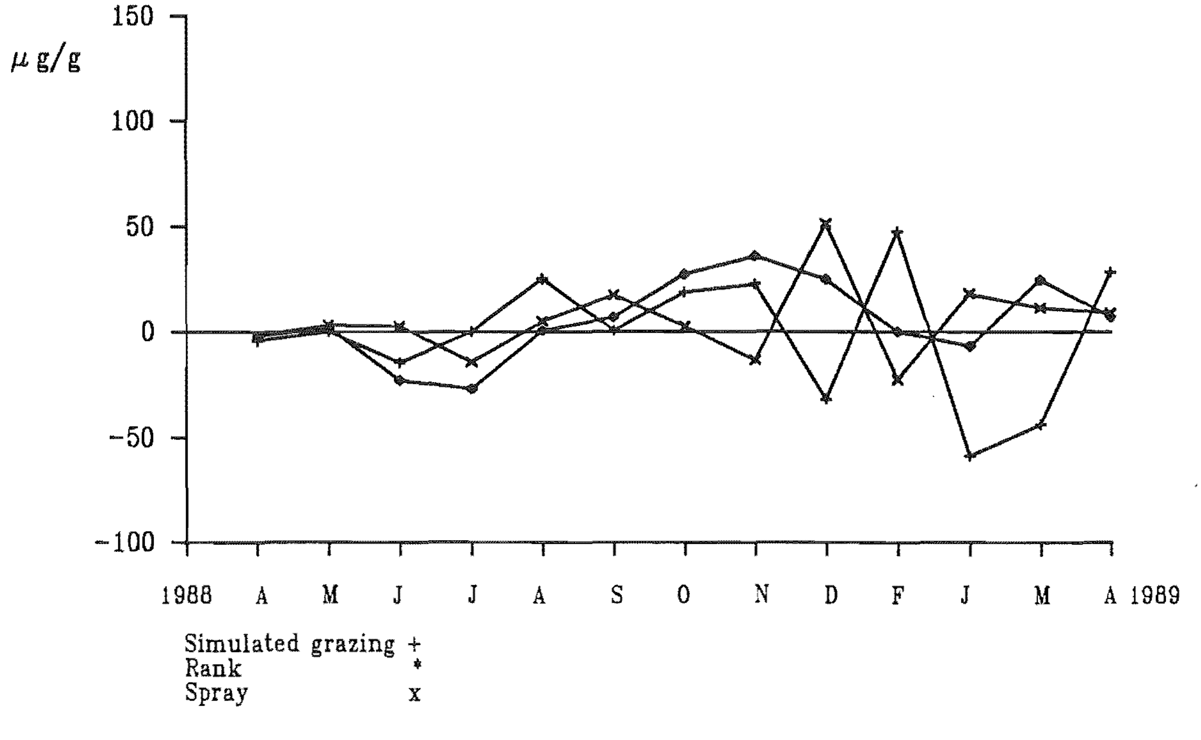


Figure 7.5b Change in NH_4^+-N concentrations in the 0-5 cm soil depth between 1 and 2.5 m radius of the stem as influenced by level of competing vegetation, April 1988-May 1989.

Net N mineralization was calculated as the difference between the quantity of total mineral N (i.e. $NH_4^+ + NO_3^-$) accumulated at the end of the incubation period minus the quantity of total mineral N ($NH_4^+ + NO_3^-$) at the start of the incubation for each depth of soil sampled.

7.3 $\quad$ $\text{Net } N_{min} = (NH_4^+\text{-}N_{a(t+1)} + NO_3^-\text{-}N_{a(t+1)}) - (NH_4^+\text{-}N_{i(t)} + NO_3^-\text{-}N_{i(t)})$

There was no significant interaction ($P < 0.5$) between sampling date x level of competing vegetation x added N on the change in NH_4^+-N concentration (ammonification) during incubation (Appendix 7.2a) in the 0-5 cm soil depth. However, the interaction between sampling date x level of competing vegetation x distance of sampling was highly significant ($P < 0.005$) (Appendix 7.2a).

For example, within 1 m of the stem, NH_4^+-N in the rank treatment nearly always accumulated during the incubation in contrast to the sprayed treatments where NH_4^+-N was nearly always immobilized during the incubation. NH_4^+-N was rarely immobilized in the simulated-grazing treatments (Fig. 7.5a). Between 1 and 2.5 m from the stem, NH_4^+-N is also often immobilized in the sprayed treatments (Fig. 7.5b). At this distance NH_4^+-N was also immobilized during incubations in the simulated-grazing treatments. During September to December, NH_4^+-N accumulated in the rank treatments.

Although NH_4^+-N concentrations were initially similar at both distances for the three levels of competing vegetation, NH_4^+-N concentrations generally increased in later incubations, especially in the September to November incubations (Figures 7.5a and 7.5b).

There was a significant interaction between the accumulation of NH_4^+-N x time ($P < 0.05$) (Appendix 7.2a) and NH_4^+-N tended to accumulate in the plus-N treatments for most incubation periods (Fig. 7.5c). Accumulation of NH_4^+-N in the no-N treatments was generally lower than in the plus-N treatments and on occasions was negative (Fig. 7.5c).

There was no significant within-subject interaction of time x level of competing vegetation x applied N on the change in NH_4^+-N concentration during the incubation in the 5-15 cm soil depth, and the interactions between time and the pasture and plus-N treatments were not significant (Appendices 7.2a and 7.2b).

Although NH_4^+-N accumulated in some treatments during the length of the *in situ* incubations, levels of accumulated N were not always positive and accumulations appeared to peak in the December incubation. Net negative ammonification during incubation can occur when the rate of nitrification exceeds the rate at which organic N is mineralized to NH_4^+-N. This is possible when NH_4^+-N pools at the start of an incubation period are large (Nadelhoffer *et al.*, 1984).

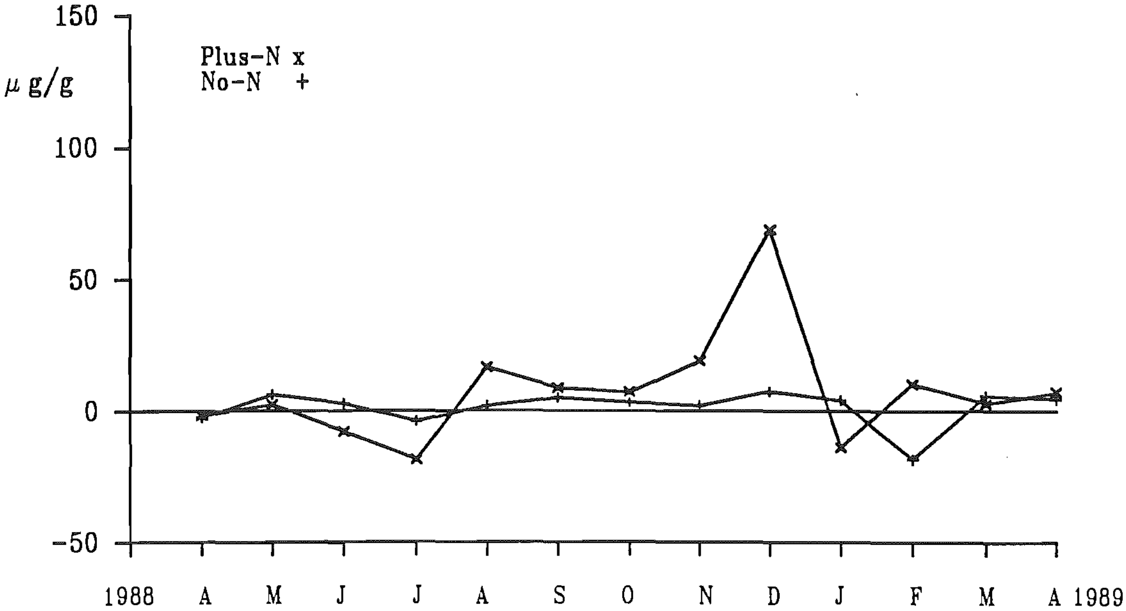


Figure 7.5c Change in NH_4^+-N concentrations in the 0-5 cm soil depth within 1 m radius of the stem as influenced by split applications of nitrogen fertilizer, April 1988-April 1989.

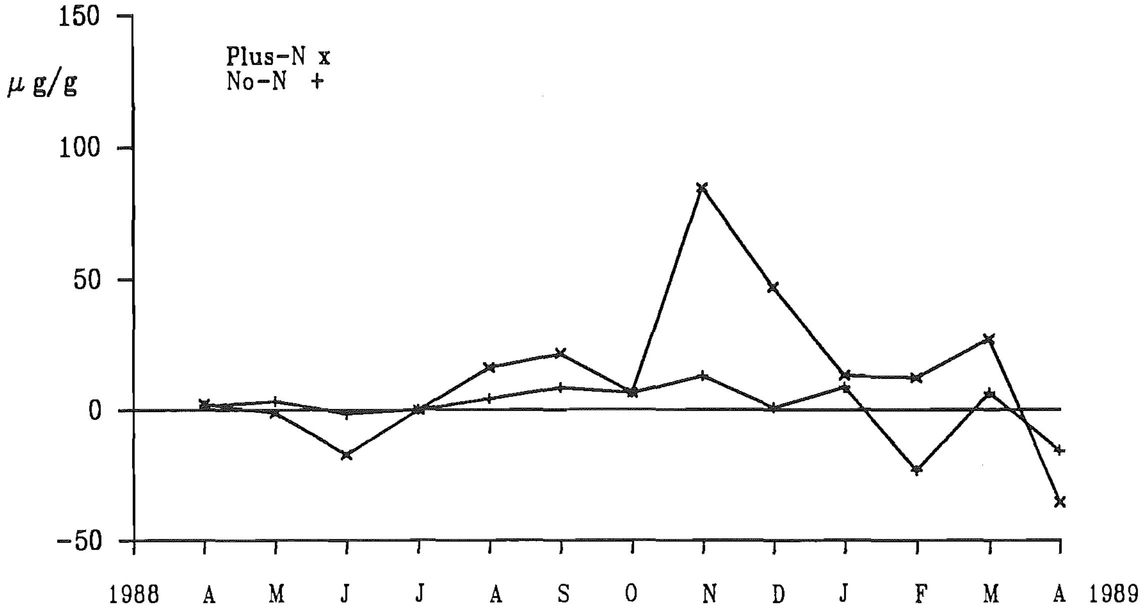


Figure 7.6 Change in NO_3^--N concentrations in the 0-5 cm soil depth within 1 m radius of the stem as influenced by split applications of nitrogen fertilizer, April 1988-April 1989.

The change in NO_3^--N concentration did not show any significant interactions between time x level of competing vegetation x added N in the 0-5 cm soil depth (Appendix 7.2a) but there was a highly significant ($P < 0.005$) interaction between sampling date and added N (Appendix 7.2a). In the plus-N treatments, except for June 1988 and April 1989 samplings, the change in NO_3^--N concentration was positive and in the no-N treatments negative changes in NO_3^--N concentration occurred in June 1988, February and April 1989 (Fig. 7.6).

Nitrification peaked in the November incubation for both plus-N and no-N treatments and were lowest during autumn and early winter when ammonification was also low (Fig. 7.5c).

In contrast to ammonification the time x distance effect for change in NO_3^--N concentration (nitrification) was not significant (Appendix 7.2a). This suggests that nitrification was proceeding at a similar rate at both distances from the stem throughout the study (Figures 7.7a and 7.7b).

Changes in NO_3^--N concentrations in the 5-15 cm soil depth showed an interaction of time x level of pasture competition ($P < 0.05$) (Appendix 7.2a). Nitrification rate varied throughout the experiment, especially for the rank treatment (Fig. 7.7c). Net nitrification, or the accumulation of NO_3^--N, occurred for all treatments except between August 1988 and January 1989. Larger quantities of NO_3^--N nearly always accumulated in the sprayed treatments. Immobilization of NO_3^--N during incubations occurred in the February 1989-April 1989 incubations. The reasons for this are uncertain but may be due to uncontrolled experimental error. However, Edmonds and McColl (1989) have also observed net NO_3^- immobilization during summer months using similar methods.

Rates of nitrification are nearly always positive because NO_3^--N pools in soils were typically small and in most cases some NH_4^+-N was oxidized to NO_3^--N during incubation.

No significant interaction ($P < 0.05$) occurred between sampling date x level of competing vegetation x added N (Appendix 7.3) for net N mineralization in the 0-5 cm soil depth between April 1988 and April 1989. However, there was an interaction at $P = 0.0598$ between sampling date and added N (Fig. 7.8). Net immobilization of N occurred in the plus-N treatments between April 1988 and August 1988 and thereafter net mineralization of N occurred except in the January 1989 and April 1989 incubations (Fig. 7.8). Net N mineralization was nearly always higher in the plus-N plots in the 0-5 cm soil depth.

Net N mineralization in the 5-15 cm soil depth was not affected by the level of competing vegetation, nor by added N, and there was no significant interaction between these two treatments but there were highly significant changes in the amount of net N mineralized between sampling dates ($P < 0.01$) (Appendix 7.3).

Net N mineralized in each incubation was summed for each treatment combination (Table 7.1) and data were statistically analyzed using ANOVA (Appendix 7.4).

The interaction between level of competing vegetation and added N was significant for total net N mineralized in the combined 0-15 cm soil depth ($P = 0.0502$). The monthly addition of N increased cumulative net N mineralization by 117% and 17.8 times in the rank and sprayed treatments, respectively, and cumulative net N mineralized declined by 22% in the simulated-grazing treatment (Fig. 7.9).

Table 7.1 Cumulative nitrogen mineralized in the 0-5 and 5-15 cm soil depths, April 1988-April 1989.

	Grazing		Rank		Sprayed		
Soil depth (cm)	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
				g N/plot[2]			
0-5	16.4	81.3	451.3	120.8	801.4	-22.0	169.06
5-15	109.6	79.4	-105.1	38.6	93.05	69.6	105.50
Total	126.0	160.7	346.2	159.4	894.5	47.6	143.12

1 Standard error.
2 Plot area = 11.341 m^2.

The added N treatment significantly increased ($P < 0.05$) cumulative net N mineralization by 272% whereas the removal of pasture competition increased cumulative net N mineralization by 138% ($P = 0.0698$).

The ANOVA of the proportion of NO_3^--N in the quantity of cumulative net mineralized N (Appendix 7.5) showed no significant effects ($P < 0.05$) (Table 7.2). On average, for all treatments, 47% of mineralized N was in the NO_3^--N form (Table 7.2).

Table 7.2 Percent NO_3^--N in net nitrogen mineralized in the incubated cores in the 0-15 cm soil depth.

Grazing		Rank		Sprayed		
Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			%			
0	27	37	69	80	69	29.9

1 Standard error.

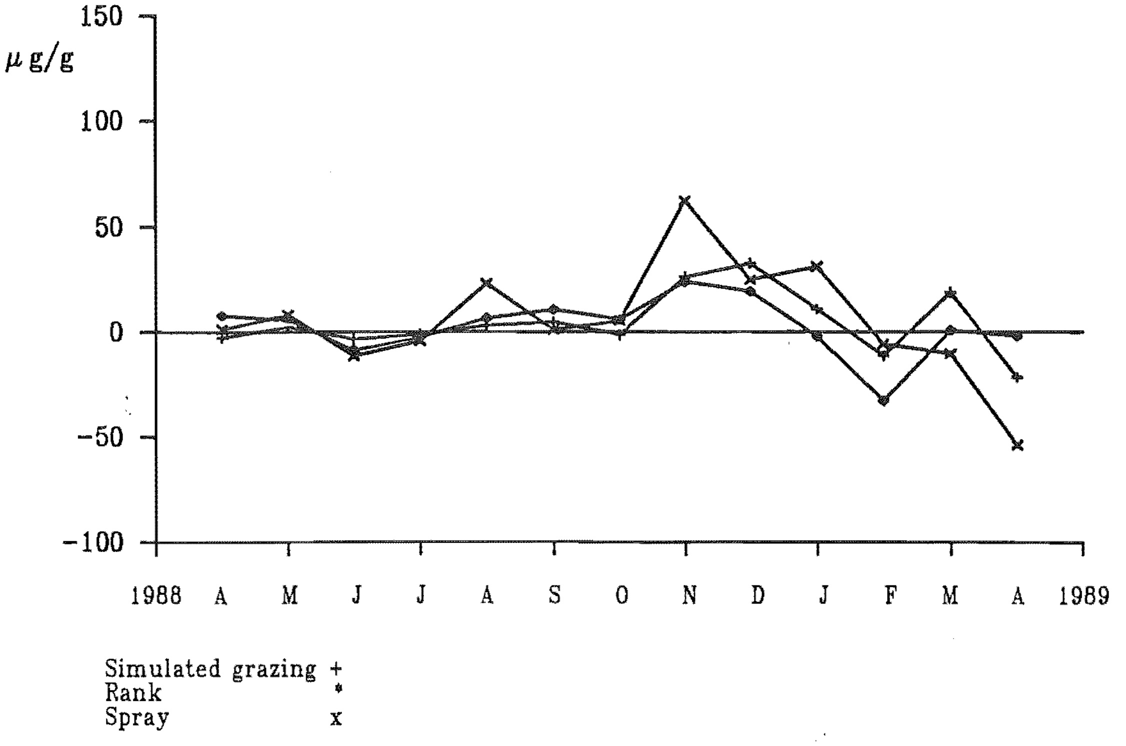


Figure 7.7a **Change in NO_3^--N concentrations in the 0-5 cm soil depth within 1 m radius of the stem as influenced by level of competing vegetation, April 1988-April 1989.**

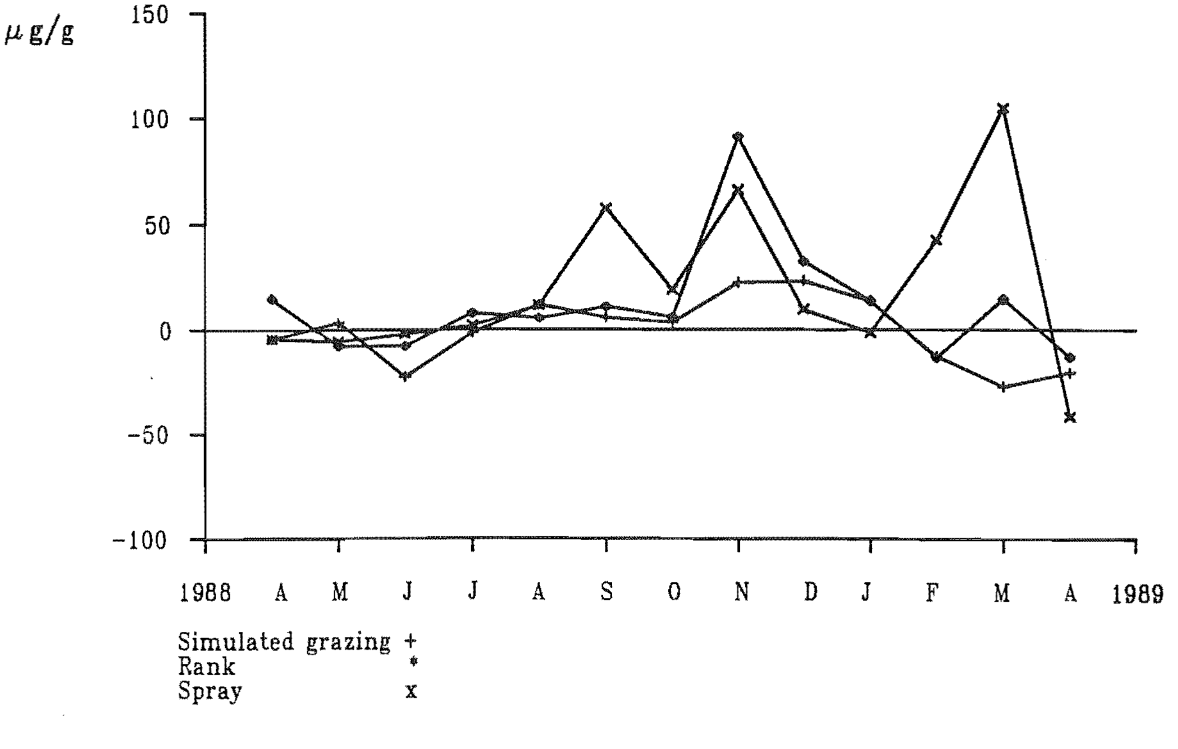


Figure 7.7b **Change in NO_3^--N concentrations in the 0-5 cm soil depth between 1 and 2.5 m radius of the stem as influenced by level of competing vegetation, April 1988-April 1989.**

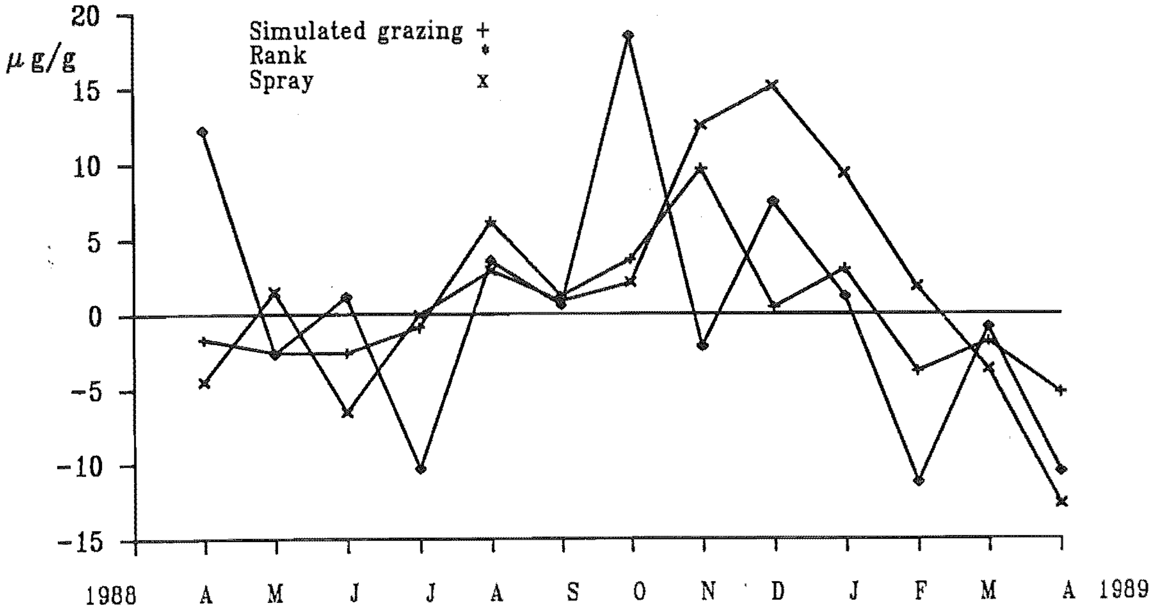


Figure 7.7c Change in NO_3^--N concentrations in the 5-15 cm soil depth as influenced by level of pasture competition, April 1988-April 1989.

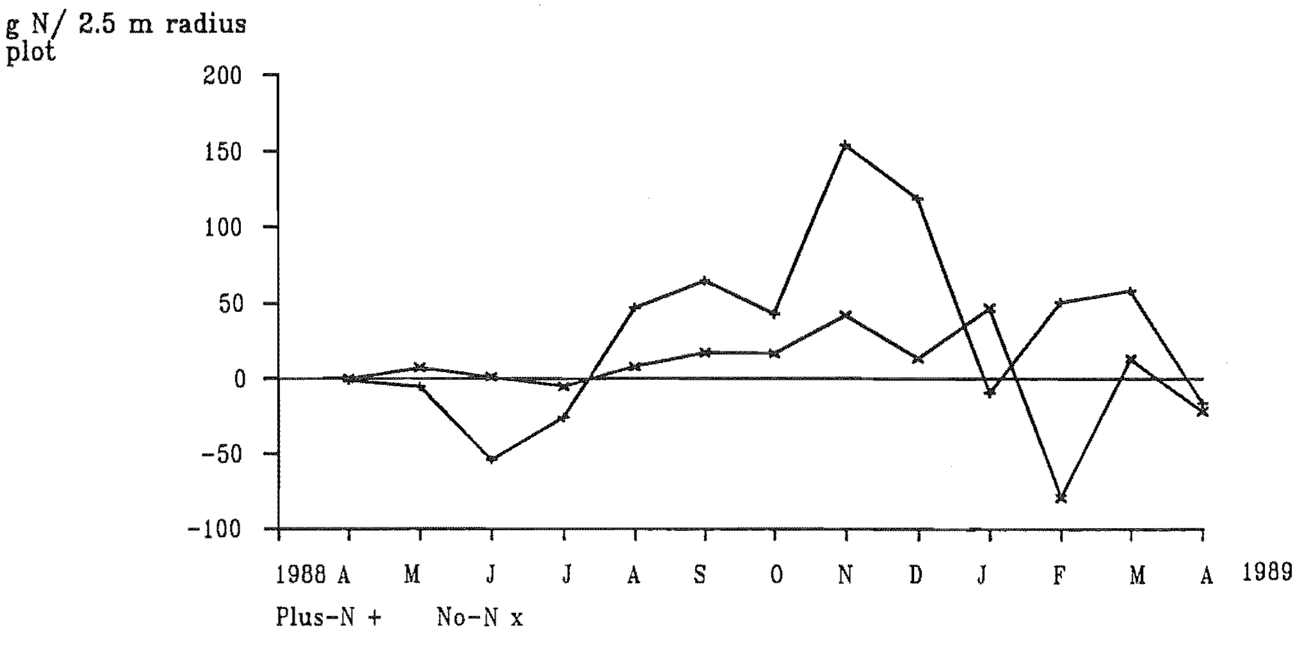


Figure 7.8 Net nitrogen mineralized ($NH_4^+ + NO_3^-$) in the 0-5 cm soil depth as influenced by split applications of nitrogen fertilizer, April 1988-May 1989.

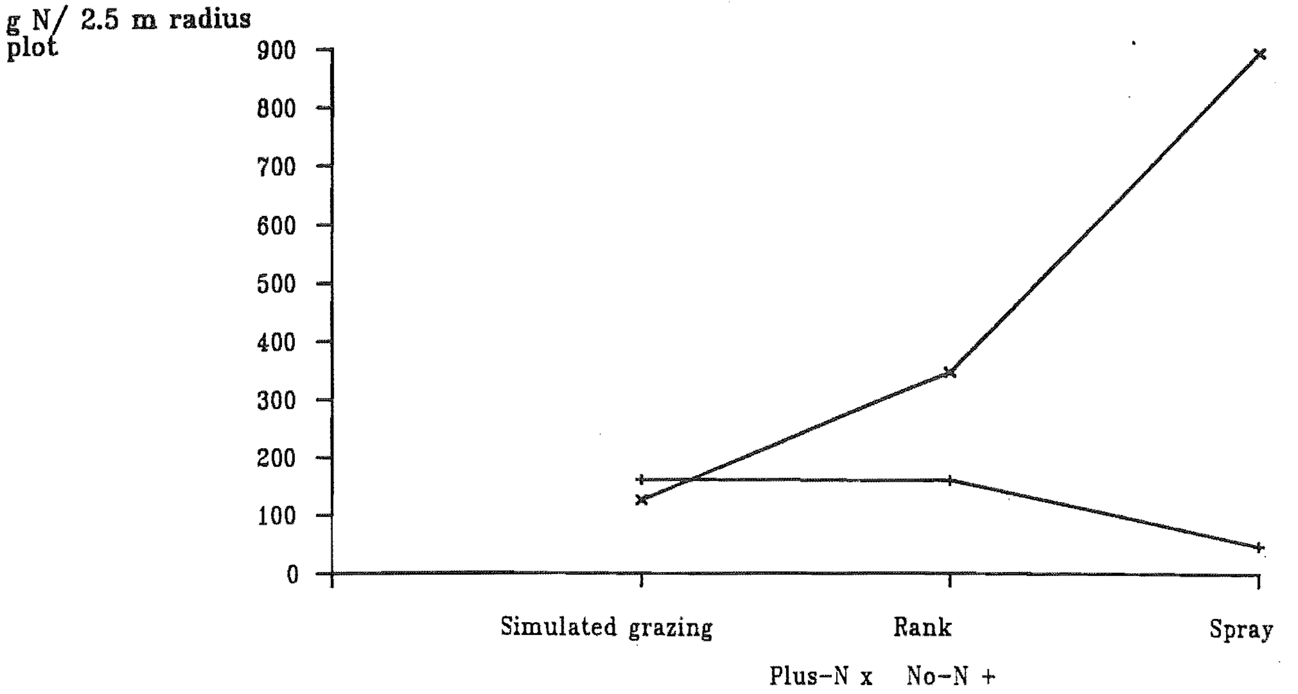


Figure 7.9 **Interaction between level of competing vegetation and added nitrogen on cumulative net nitrogen mineralized in the 0-15 cm soil depth, April 1988-May 1989.**

7.4 Nitrogen uptake

In Section 7.3 the quantity of net N mineralized was calculated (Table 7.1). However, the form of mineral N made available to trees may counteract the effects of seasonal net N mineralization patterns (Nadelhoffer *et al.*, 1984). They reported that when NH_4^+-N pools are sufficiently large, nitrification and NO_3^- uptake may occur even during periods when net N mineralization is low or close to zero. It is therefore possible to calculate N uptake by vegetation if it is assumed that net N mineralization and nitrification rates in incubated soils are good estimates of actual rates in surrounding undisturbed field soils (Nadelhoffer *et al.*, 1984).

To do this Nadelhoffer *et al.* used the following equations:

$$\textbf{7.4}\ NH_4^+\text{-}N_{upt} = NH_4^+\text{-}N_{a(t+1)} - NH_4^+\text{-}N_{i(t+1)}$$

$$\textbf{7.5}\ NO_3^-\text{-}N_{upt} = NO_3^-\text{-}N_{a(t+1)} - NO_3^-\text{-}N_{i(t+1)}$$

$$\textbf{7.6}\ N_{upt} = NH_4^+\text{-}N_{upt} + NO_3^-\text{-}N_{upt}$$

Where $NH_4^+\text{-}N_{i(t+1)}$ = mean NH_4^+-N content of non-incubated soil at end of interval t.
$NO_3^-\text{-}N_{i(t+1)}$ = mean NO_3^--N content of non-incubated soil at end of interval t.
$NH_4^+\text{-}N_{upt}$ = NH_4^+-N uptake between t and t+1
$NO_3^-\text{-}N_{upt}$ = NO_3^--N uptake between t and t+1
N_{upt} = total N uptake between t and t+1

Estimates of N taken up using these equations are shown in Table 7.3. However, because the monthly addition of N was made after the incubations had been established it was not appropriate to estimate N uptake in the plus-N treatments using this approach. If, when calculated, monthly $NH_4^+\text{-}N_{upt}$ or $NO_3^-\text{-}N_{upt}$ was negative this was assumed to be an artifact due to sampling error and percent N uptake was assumed to be zero (see Nadelhoffer *et al.*, 1984).

Nitrogen uptake calculated using Equations 7.4 to 7.6 for rank and sprayed treatments was higher than estimated using the difference between (NH_4^+ + NO_3^-) before and after incubation (Section 7.3). The difference between the two methods in estimating N uptake in the spray-no-N treatments highlights the need to assess the form of mineral N available for plant uptake. Overall changes in mineral N may be low but, if nitrification has occurred, soil NH_4^+-N pools can decline with no net change or only a small change in total mineral N.

Table 7.3 Cumulative nitrogen uptake calculated assuming mineralization rates in cores are good estimates of rates in surrounding soil in the 0-5 and 5-15 cm soil depths, April 1988-April 1989.

		Grazing		Rank		Sprayed	
	cm	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N
				g N/2.5-m-radius plot			
NH_4^+	0-5	254.5	100.1	190.5	98.6	249.3	90.85
	5-15	7.4	6.1	26.3	33.9	18.4	14.25
	Total	261.9	106.2	216.8	132.5	267.7	105.1
NO_3^-	0-5	160.3	53.4	408.4	67.6	216.8	179.35
	5-15	58.9	27.3	65.4	51.1	55.2	30.4
	Total	219.2	80.7	473.8	118.7	272.0	209.75
NH_4^+ + NO_3^-		481.1	186.9	690.6	251.2	539.7	314.85
%NO_3^-		45.6	43.2	68.6	47.3	50.4	66.6

7.5 Apparent nitrogen uptake

Nitrogen uptake by vegetation can also be estimated by measuring the fluxes of N into and out of the available N pool in the soil (Nadelhoffer *et al.*, 1985; Dyck *et al.,* 1987; Raison *et al.*, 1987) using the equation:

$$7.7\ N_u = N_m + N_i - N_L - N_s$$

where N_u = apparent N uptake, or inorganic flux from available soil N pool to vegetation

N_m = net N mineralized

N_i = inputs of inorganic N - via precipitation or throughfall

N_L = N leached below effective rooting depth

N_s = increment in inorganic soil N during study period.

Fluxes of inorganic N in precipitation or in throughfall and leaching or gaseous loss were not measured in this study. However, such fluxes will be small compared to those applied artificially in this experiment to four of the six treatments where N was applied either as return of some N in clippings removed in the simulated-grazing treatment and/or the monthly addition of N (Table 7.4).

Table 7.4 Apparent nitrogen uptake from the 0-15 cm soil depth into a tree and pasture in a 2.5-m-radius plot with a tree at its centre; using the equation $N_u = N_m + N_i - N_s$.

		N_u	=	N_m	+	N_i	-	N_s
				g N/plot				
Grazing	Plus-N	252		126		506		380
	No-N	207		161		106		60
Rank	Plus-N	557		346		388		177
	No-N	160		159		0		-1
Spray	Plus-N	876		895		388		407
	No-N	-28		48		0		76
S.E.[1]		108.4		143.1		-		85.8

1 Standard error.

If it is assumed that N_i is the quantity of N added during the length of the experiment, N_u (Table 7.4) can be estimated using estimates of N_m (Section 7.3) and N_s (Table 7.5). All weights are expressed as g N/2.5-m-radius plot with a tree at its centre and to a depth of 15 cm.

Apparent N uptake by *P. radiata* and pasture ranged from 876 to -28.4 g nitrogen per 2.5-m-radius plot (Table 7.4). There was a significant interaction between level of competing vegetation and applied N (Fig. 7.10, Appendix 7.6).

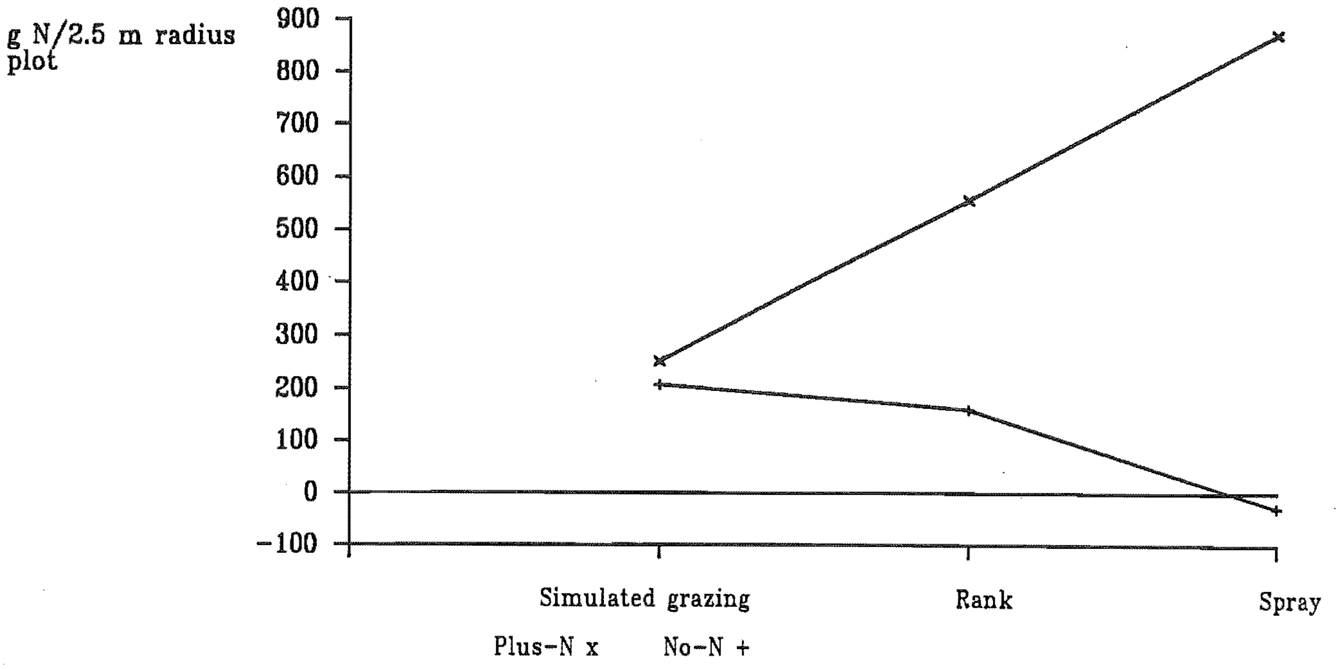


Figure 7.10 Effect of level of competing pasture and added nitrogen on apparent nitrogen uptake into trees and pasture, April 1988-May 1989.

Addition of N increased apparent N uptake at the three levels of competing pasture on average by four times. The biggest increase of 32 times occurred in the sprayed treatment.

Estimates of N uptake into the aboveground biomass of trees and pasture were made as a basis for comparison with the N mineralization method (Dyck *et al.*, 1987; Smethurst and Nambiar, 1989). Nitrogen uptake by the trees at the centre of the plots used in the N mineralization study was calculated as final N content aboveground tissues - initial aboveground N content (Appendix 3.16a). Nitrogen uptake by pasture in the simulated-grazing and rank treatments was estimated from the sum of N in successive harvests (simulated-grazing treatments) removed from a 1.9-m-radius circle around the central tree or N removed from a similar area in the rank treatments at the end of the experiment (Table 5.4). This quantity was converted to a m^2 basis and quantities of N were recalculated for the 2.5-m-radius plot. The interaction ($P < 0.05$) between level of competing vegetation and added N was not significant and there were no significant treatment effects (Table 7.6, Appendix 7.6).

Nitrogen uptake estimates from both the biomass method and the apparent N uptake method were compared using a paired T-test (Table 7.7), and although the mean difference between the two methods was 71 g N/plot this was not

Table 7.5 **Increment in inorganic nitrogen during the study period in both 0-5 and 5-15 cm soil depths, April 1988-April 1989.**

	Grazing		Rank		Sprayed		
cm	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			g N/plot[1]				
0-5	289.3	30.1	125.7	1.6	253.0	77.8	60.25
5-15	90.7	29.4	51.6	-2.5	154.2	-2.1	32.46

1 Plot radius = 2.5 m.

Table 7.6 **Nitrogen uptake in aboveground tree and pasture biomass, August 1988-April 1989.**

Grazing		Rank		Sprayed		
Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
		g N/ 2.5-m-radius plot				
451	264	289	230	134	229	83.0

1 Standard error.

Table 7.7 **Summary paired T-test for nitrogen uptake estimates from biomass and apparent nitrogen uptake methods.**

Aboveground biomass N uptake	Apparent N uptake	S.E.[1]	P[2]
266	337	105.9	0.5167

1 Standard error.
2 Probability from paired T-test that the mean of the difference is zero.

significant. The standard error for the differences was high due to the uncontrolled experimental errors. Trees were of different sizes and due to low replication ANCOVA could not be used. Differences between the two methods may have been reduced further if estimates of N uptake into roots and shoots, N uptake into pasture between April 1988 and August 1988 and leaching losses had been made.

It is possible that in some cases differences between the methods would increase especially when combined tree and pasture aboveground N uptake was greater than any estimate of N uptake made from indirect methods. Where N uptake into the aboveground biomass of trees plus pasture (Table 7.6) exceeds the estimate of apparent N uptake (Table 7.4), the difference may represent biological N fixation. Clover dominated grasses in the earlier harvests when most N was removed as clippings (Chapter Five).

7.6 Summary

- There are several aspects of the in situ N mineralization method that reduce its utility as a routine method. In particular, the method is limited when used without prior knowledge of the situation in question. Whilst good agreement was shown between the estimates of apparent N uptake and aboveground plant N uptake in this experiment, experimental error was large. Increased replication may help reduce the errors and the inclusion of belowground plant N uptake into the estimates based on biomass sampling would have given even closer agreement, as would have inclusion of other inputs and outputs (volatilization, denitrification, rain) in the apparent N uptake calculation. However, even with this data, agreement is not always good (Dyck *et al.*, 1987).

  The main area of concern with the mineralization method arises because of similarity between conditions inside and outside the bag during incubation. Firstly, soil moisture conditions may vary inside and outside the bag and, in this study and other reported studies, no attempt was made to control this variability. Secondly, severed roots may initially immobilize inorganic N inside cores but, if conditions are suitable, inorganic N may be released with time.

  Another problem that exists is that N mineralization may occur below the depth studied but it is not possible to sample the entire soil profile exploited by roots.

  It has also been reported elsewhere that length of incubation period affects the accumulation of mineral N. Short-term incubations are therefore preferred (Adams *et al.*, 1990). In this study N fertilizer was applied after the incubation had been established, although this did not have a significant effect on conditions outside the bag.

  The third alternative is to use labelled N. The use of ^{15}N reduces some of the sampling variability and also allows quantification of important ecosystem processes such as immobilization. It must be remembered that the method, as used here, only measures uptake of applied ^{15}N. The ^{15}N method also allows for easy partitioning of applied N into that taken up by trees and pasture, something that cannot be done by the in situ N mineralization method. ^{15}N can be used to trace successive uptake of N by plants and changes in pool sizes of available soil N, and allows the origin of plant and soil N to be followed.

Proponents of the in situ N mineralization method have claimed that the expense and intensive sampling required when using ^{15}N limits its use. However, the quality and reliability of ^{15}N data and the increased understanding of the system can be justified because the method allows **processes that regulate** N mineralization to be examined rather than simply the **outcome** of N mineralization.

- Ambient soil mineral N concentrations were high especially in the plots that received N.

- Mineral-N concentrations were nearly always higher **between** 1 and 2.5 m radius of the tree than **within** 1 m radius of the tree.

- Sprayed treatments generally had the highest mineral-N concentrations at all sampling dates.

- Rates of ammonification were generally higher **between** 1 and 2.5 m radius than **within** 1 m radius of the tree at all sampling dates.

- Rates of ammonification and nitrification were generally higher in the plus-N treatments than in the no-N treatments at all sampling dates.

- Net N mineralization was generally higher in the plus-N treatments at all sampling dates.

Chapter Eight

Soil moisture dynamics

8.1 Introduction

Soil moisture dynamics in the surface 10 cm of soil were followed on a monthly basis using gravimetric soil sampling. Deeper in the soil profile, dynamics were monitored on a weekly basis using a neutron moisture meter to record soil moisture volume fraction (θ)[1]. Two sampling locations were established at 1 m and 2.5 m from the trees.

The neutron moisture meter data presented here were calibrated with laboratory measurements at 35 and 100% moisture by volume (R.J. Jackson, Forest and Wildlands Ecosystem Centre, Forest Research Institute, Christchurch, pers. comm.). Agreement between values determined for volumetric soil samples taken at the time of installation of eight access tubes and initial neutron moisture metre readings was good (Appendix 2.5).

The purpose of the soil moisture monitoring program was to assess the effect of removing competing vegetation on soil moisture dynamics. This aspect of the study assisted in the interpretation of the competition between *P. radiata* and pasture and the underlying influences of removing competing vegetation in the sprayed treatment.

8.2 Soil moisture volume fraction (θ) in the surface 10 cm of soil

The neutron moisture meter cannot be used for measuring changes in soil moisture content in the surface soil due to loss of neutrons from the soil surface (Greacen, 1981). Therefore, the dynamics of soil moisture in the surface 10 cm of soil were monitored by assessing soil moisture content in cores collected as part of the N mineralization study. For the purpose of analysis, samples were grouped as either 1 m or 2.5 m from the stem.

There was no significant time x treatment x distance from the tree interaction for moisture volume fraction (θ) in the top 10 cm of surface soil between April 1988 and May 1989 (Appendix 8.1) although the interaction between time and distance from tree was significant ($P < 0.01$) (Fig. 8.1a, Appendix 8.1).

1 Soil moisture volume fraction (θ) is expressed as m^3 water/m^3 soil.

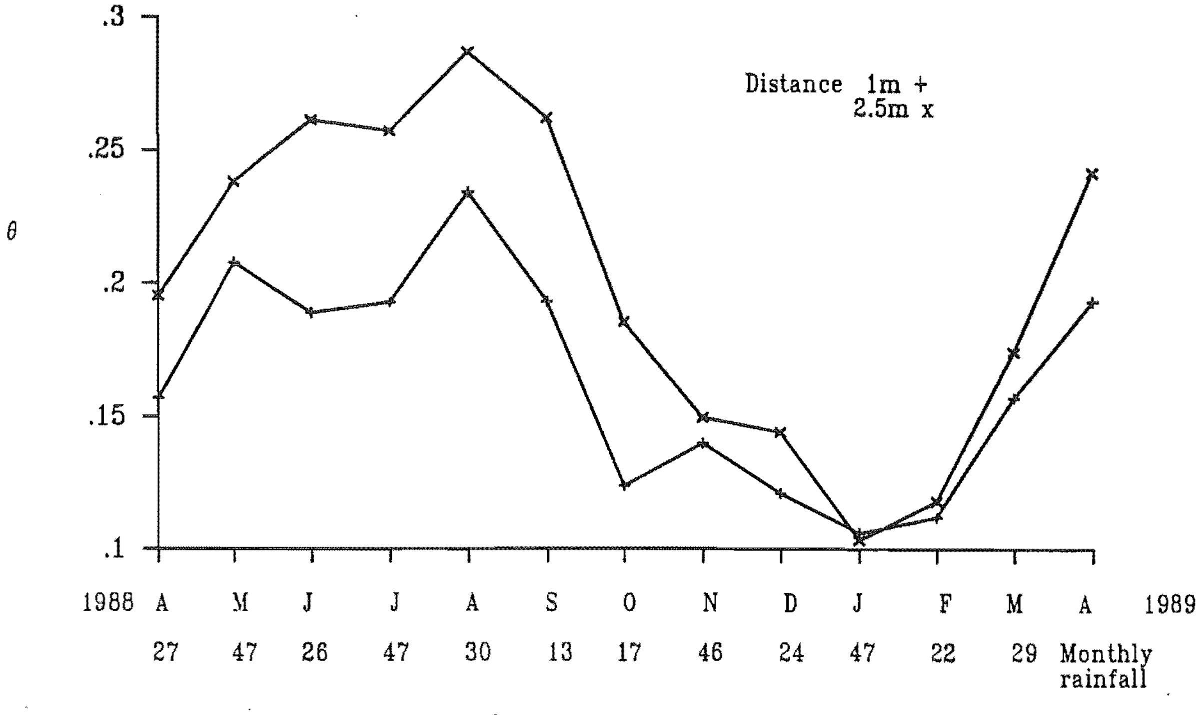


Figure 8.1a **Moisture volume fraction in the 0-10 cm soil depth at the 1 m and 2.5 m locations, April 1988-April 1989.**

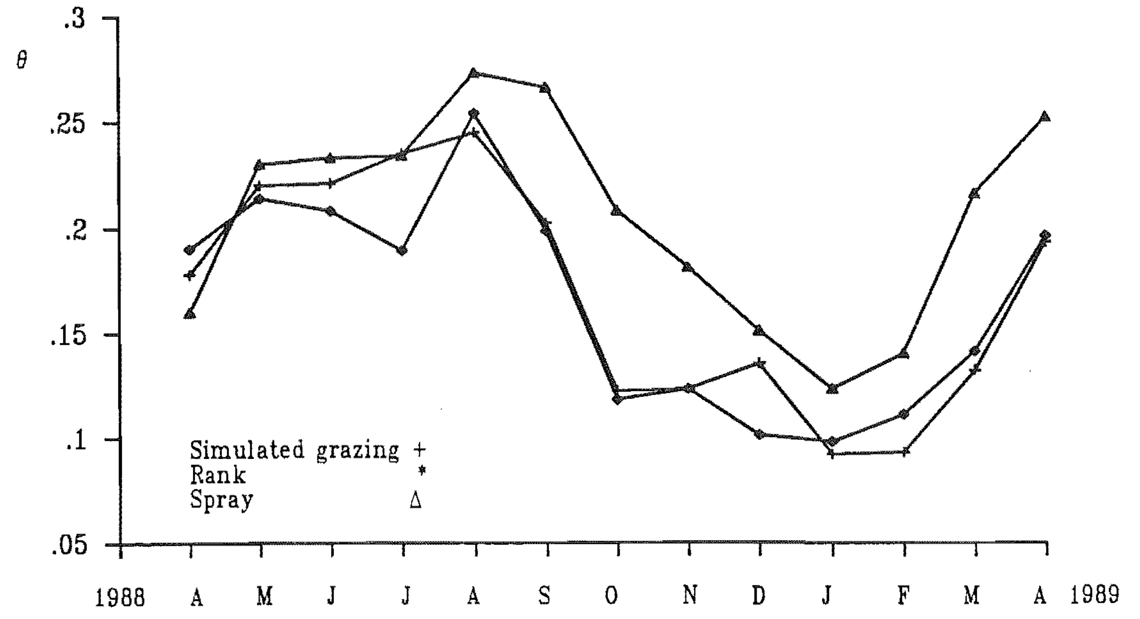


Figure 8.1b **Moisture volume fraction in the 0-10 cm soil depth as influenced by level of pasture competition, April 1988-April 1989.**

Soil moisture volume fraction peaked at both 1 m and 2.5 m from the tree in August and thereafter declined until February when it began to increase again in all treatments. The decline in θ was independent of level of pasture competition (Appendix 8.1) and θ increased faster at 2.5 m from the trees after January.

In spring, during the time of ^{15}N application and maximum pasture production rate (Fig. 3.4), θ declined rapidly especially at 1 m from the stem.

At the beginning of October, θ measured at 1 m from the trees was only 66% of the value at 2.5 m distance from the trees. By November, θ at 1 m was 93% of the 2.5 m value.

This period of rapid decline (September-November) in θ corresponds to a period of low rainfall (22.3 mm from 12 September to 30 October 1988) and low humidity (Section 2.2) and declining pasture production (Section 3.3.1). Soil moisture volume fraction was always lower at 1 m from trees than at 2.5 m from trees at all sampling times.

Table 8.1 **Soil moisture volume fraction in the 0-10 cm soil depth at the 1 and 2.5 m locations as influenced by pasture competition, April 1988-April 1989; treatment means.**

	Simulated-grazing		Rank		Spray	
	1 m	2.5 m	1 m	2.5 m	1 m	2.5 m
			θ			
April	0.150	0.205	0.173	0.225	0.150	0.171
May	0.204	0.235	0.206	0.232	0.215	0.245
June	0.204	0.239	0.174	0.275	0.189	0.276
July	0.222	0.248	0.157	0.253	0.199	0.269
August	0.223	0.268	0.231	0.302	0.248	0.298
September	0.172	0.234	0.166	0.263	0.242	0.289
October	0.104	0.140	0.102	0.150	0.166	0.249
November	0.125	0.120	0.111	0.149	0.184	0.179
December	0.129	0.142	0.100	0.104	0.135	0.167
January	0.096	0.088	0.099	0.096	0.124	0.123
Febuary	0.097	0.088	0.107	0.121	0.132	0.147
March	0.139	0.126	0.137	0.150	0.196	0.235
April	0.179	0.207	0.187	0.214	0.214	0.290
Overall mean	0.157	0.180	0.150	0.195	0.184	0.226

The interaction between time and level of pasture competition was also significant ($P < 0.005$) (Fig. 8.1b, Appendix 8.1). Except for the first sampling, sprayed treatments were always wetter than plots with pasture, and did not dry out as fast during the very dry months of September and October. These treatments also re-wet considerably faster during February when 22 mm of rain fell.

The dynamics of θ were similar in the rank and simulated-grazing treatments and the only marked difference occurred during June when surface soil in the rank treatment was drier than in other treatments. There was no apparent reason for this.

The interaction between level of pasture competition and distance from the tree was significant at $P = 0.0550$ (Table 8.1). On average the sprayed treatment was wetter at both locations compared with the plus-pasture treatment.

8.3 Soil moisture content in subsurface soil

For the statistical analysis of neutron moisture meter data, soil water content between 10 and 100 cm depth, expressed as soil moisture deficit, was calculated for each tube between 15 September 1988 and 29 April 1989. Because of the lack of replication treatments were pooled into four groups: with or without pasture, and with tubes 1 or 2.5 m from the tree (Table 8.2).

Table 8.2 Number of tubes in each group used to analyze soil moisture deficit in the 10-100 cm soil depth.

	Plus-pasture		No-pasture	
Location	1 m	2.5 m	1 m	2.5 m
	Number of tubes			
	4	5	3	3

There was no significant interaction between level of pasture competition and distance from a stem for the soil moisture deficit measured on 15 September 1988 (Table 8.3, Appendix 8.2). However, the soils were drier close to the tree ($P = 0.0052$).

There was a highly significant interaction between time x level of pasture competition x distance from the stem (Fig. 8.2, Appendix 8.3).

Table 8.3 **Soil moisture deficit on 15 September 1988 in the 10-100 cm soil depth.**

	Plus-pasture		No-pasture		
Location	1 m	2.5 m	1 m	2.5 m	S.E.[1]
		mm H_2O			
	108	79.4	94	34	9.2

[1] Standard error.

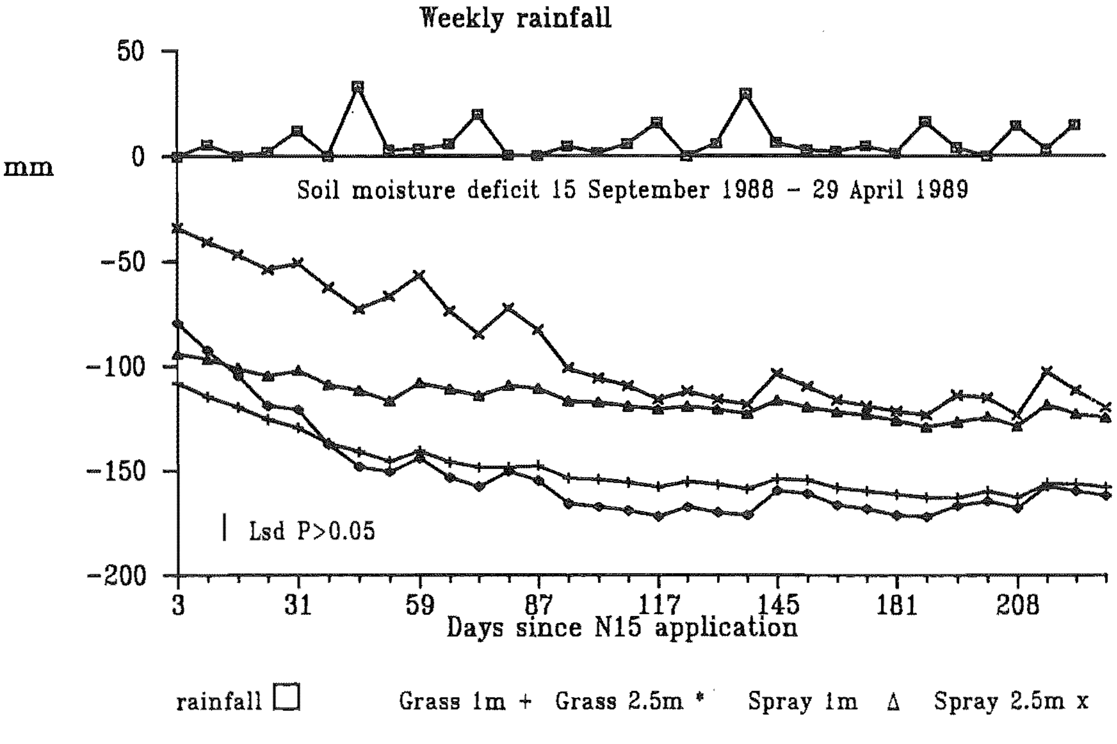


Figure 8.2 Weekly rainfall and seasonal course of soil water deficit in 10-100 cm soil depth at 1 m and 2.5 m from tree, 15 September 1988-29 April 1989.

Removing pasture competition reduced soil moisture deficit, both at 1 m and 2.5 m from a stem (Fig. 8.2), and at all times the no-pasture treatment was significantly wetter at both positions. Where pasture was present water was lost rapidly at 2.5 m from the tree so that by Day 38 the soil moisture deficit (133 mm) was equal to that at the 1 m location. This pattern did not happen in the no-pasture treatment until Day 117 when the soil moisture deficit was 120 mm.

There were no significant differences in the overall change in soil moisture deficit in the 10-100 cm soil depth due to the removal of competing vegetation ($P > 0.05$) (Table 8.4, Appendix 8.4). However, the overall changes in soil moisture deficit measured at 1 m from the tree were significantly lower than those measured at 2.5 m from a tree ($P < 0.01$) (Appendix 8.4).

Changes in θ at 2.5 m indicate soil moisture dynamics over a much larger area of the plot than the data collected at 1 m, and so may represent larger changes in soil moisture storage. At 1 m, the representative area is smaller and changes in θ are also smaller suggesting small changes in soil moisture storage directly under trees compared with those changes between trees. Rainfall patterns also influenced soil moisture deficit; the effect, which is reflected by short term fluctuations, was most pronounced at 2.5 m from the trees where grass had been kill-sprayed (Fig. 8.2).

Table 8.4 Change in soil moisture deficit, 15 September 1988-29 April 1989, in the 10-100 cm soil depth.

Plus-pasture		No-pasture		
1 m	2.5 m	1 m	2.5 m	S.E.[1]
		mm H_2O		
50	83	31	86	9.2

1 Standard error.

8.4 Soil moisture volume fraction

The changes in θ at the two distances from the tree only represented point samplings and did not integrate the continuum of θ along the radius between the two tubes. However, the data illustrated the pattern of θ changes with soil depth at different distances from the trees.

From November onwards in the simulated-grazing treatment the pattern of extraction of water at both 1 m and 2.5 m from the tree was similar (overlay Fig. 8.3a on Fig. 8.3b). At this time, surface moisture was depleted and the soil moisture deficit for 10-100 cm soil depth was 150 mm water, equal to 50% of field capacity. From November onwards most extraction occurred lower in the soil profile.

The profiles of moisture volume fraction (θ) demonstrated that plots without pasture were wetter at the start of the period, September 1988-April 1989 (overlay Figures 8.4a and 8.4b, on 8.3a and 8.3b). Furthermore, neutron moisture meter readings during the 1988 winter indicated that θ in the 10-100 cm depth of soil had not approached field capacity (Appendix 8.5).

Maximum θ in the 10-50 cm depth was recorded on 25 August readings for most tubes, although some had peaked on 21 July, while in the 50-100 cm soil depth the peak was usually at the 15 September measurement.

A comparison of soil moisture profiles at 1 and 2.5 m from the stem for sprayed-plus-N and simulated-grazing-plus-N treatments using initially similar trees in adjacent plots (root collar diameter 12.7 cm and 11.1 cm, respectively) showed that on 15 September, at 1 m from the stem, soils in the sprayed plots were wetter in the surface 20 cm than in plots with pasture. Results were similar at 2.5 m from trees. By the end of the experiment sprayed plots were still wetter at both distances from the tree. Below 30 cm depth, both treatments at 1 m distance had similar θ, but plots with pasture dried out more quickly than sprayed plots. At 2.5 m from the trees, sprayed plots were initially wetter at greater than 30 cm depth, but θ declined to similar levels with time.

8.5 Summary

Soil moisture volume fraction in the top 100 cm of soil declined rapidly during the period of rapid pasture and tree growth. Although θ increased in the top 10 cm of soil after the January sampling the soil moisture deficit in the 10-100 cm soil depth showed no increase.

Removing competing pasture had two effects on soil moisture. Firstly, removing competing pasture made the top 100 cm of soil wetter than in plots that had pasture, and secondly, soils in these plots remained wetter longer. It appeared that pasture competed directly with the trees for water but also indirectly through canopy processes that reduced soil wetting and hence reduced soil moisture storage.

It was difficult to deduce which of these two aspects had the more debilitating effect on tree growth but in this experiment the presence of pasture during a relatively dry winter reduced soil moisture storage considerably. This may in turn have reduced tree growth - an effect that would be compounded by competition for water during the following dry growing season.

The reduction in pasture dry matter production (Section 3.3.1) coincided with the period of rapid drying of soil. However, it was not possible to isolate the effects of competition between trees and pasture due to the indirect effects of pasture on soil moisture deficit. It was however apparent that as soils dried a considerable rain shadow effect developed (Fig. 8.5).

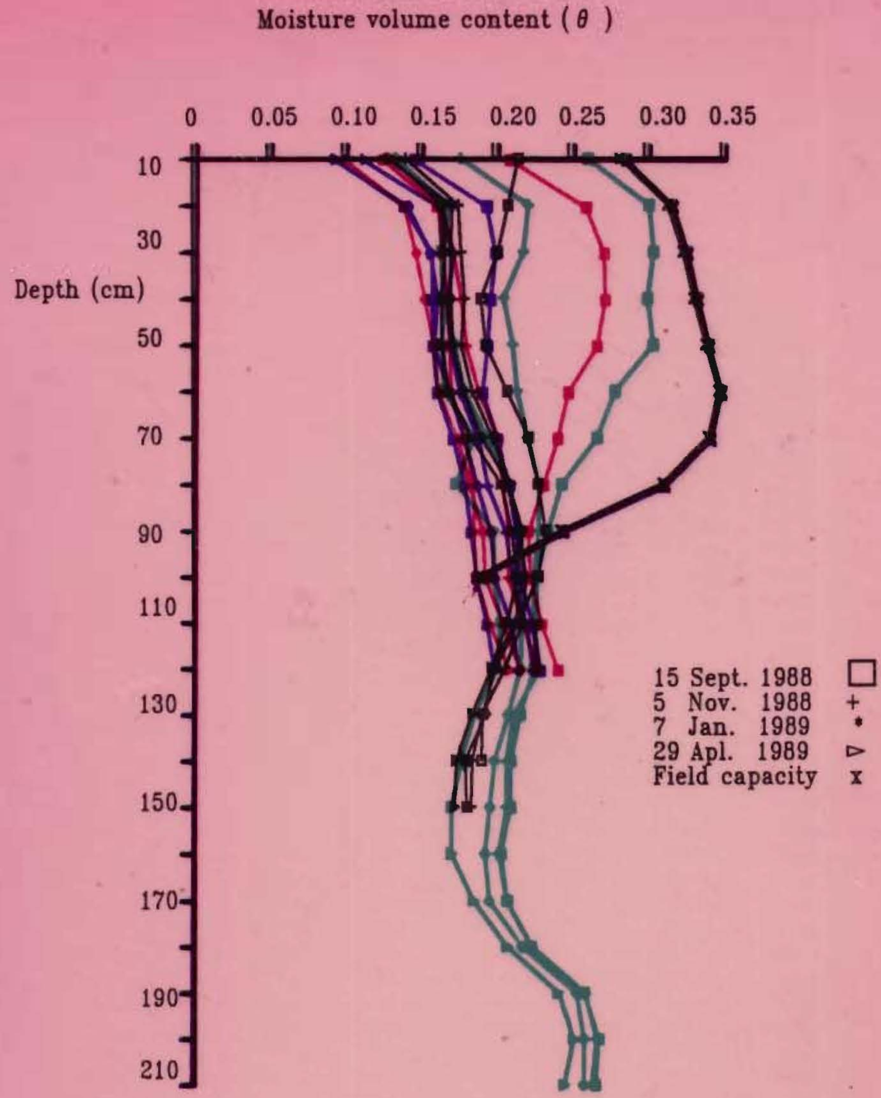


Figure 8.3a Example profile of changes in θ with soil depth, 15 September 1988-29 April 1989, 1 m from stem in simulated-grazing treatment.

Figure 8.3b Example profile of changes in θ with soil depth, 15 September 1988-29 April 1989, 2.5 m from stem in simulated-grazing treatment.

Figure 8.4a Example profile of changes in θ with soil depth, 15 September 1988-29 April 1989, 1 m from stem in a sprayed plot.

Figure 8.4b Example profile of changes in θ with soil depth, 15 September 1988-29 April 1989, 2.5 m from stem in a sprayed plot.

Figure 8.5 Example of rain shadow effect in simulated-grazing treatment showing marked zonation of pasture around trees. Wet side is on southerly aspect.

In this experiment removing competing pasture cover in autumn increased soil moisture storage for this treatment during the winter. However, had competition not been eliminated until spring, the outcome of the experiment may have been different with soil not having been re-wet to the same extent, and tree growth during spring would have been consequently reduced. However, the sprayed plots were obviously wetter all the time but could have dried out more had they started at a lower level.

Because θ was greater after the dry winter in treatments where competing vegetation had been removed, trees in these plots would have had more water available to start growing in the spring. Combined with an absence of competition, the trees were able to grow better but in doing so they removed a similar quantity of water from the soils in the sprayed treatments as in treatments with trees and pasture.

Soil moisture deficit increased rapidly during the period of rapid height growth of *P. radiata*. This period also corresponded with maximum pasture production rates in the simulated-grazing treatment and, although not measured, it corresponded with the period of rapid growth of rank pasture. Height growth in treatments with competing pasture slowed during the period November-December, which corresponded to the period where soil moisture deficit approached its maximum value in these treatments while height growth continued longer in the sprayed treatments.

Chapter Nine

Trenching experiment

9.1 Introduction

A trenching experiment was located in the simulated-grazing treatment to examine the competition between pine and pasture roots. The experiment was designed to have pasture growing with and without the influence of pine roots in order to investigate their effect on uptake of applied ^{15}N.

Three variables were measured to assess the outcome of this experiment: dry matter production, N uptake, and recovery of ^{15}N inside and outside the trenched areas.

9.2 Dynamics of dry matter production and nitrogen removal in trenched and untrenched plots

Dry matter production inside and outside the trenched areas was assessed on eight occasions from September 1988 until September 1989 (Fig. 9.1). The only significant ($P < 0.05$) effect was that associated with sampling date (Appendix 9.1), which reflected the influence of seasonal changes on dry matter production.

While the trenching treatment had no significant effect on dry matter production (Appendix 9.1b), on average, the trenching treatment increased dry matter production by 16%. Analysis of variance of weight of total dry matter removed (Appendix 9.2) also showed that there were no significant effects (Table 9.1, Appendix 9.2).

Overall, the main treatment effects of trenching or monthly addition of N alone did not significantly alter the N concentration of pasture (Appendix 9.1). However there were highly significant ($P < 0.005$) changes between sampling dates, the level dropping steadily between 14 days after ^{15}N application and 154 days and rising again in late summer and autumn (Fig. 9.2). At the final harvest, 382 days after application, N concentration was diluted by the early spring growth.

Similarly, N removed in clippings also showed significant time effects (Fig. 9.3, Appendix 9.1). Analysis of variance of the total quantity of N removed in pasture clippings (Appendix 9.2) showed that the trenching and monthly addition of N had no significant treatment effects ($P < 0.05$) (Table 9.1). However, on average, trenched plots had more than 18% more N removed in clippings than untrenched plots.

Table 9.1 **Total dry matter and nitrogen removed from pasture in trenched and untrenched plots, August 1988-September 1989.**

Plus-N		No-N		
Trenched	Untrenched	Trenched	Untrenched	S.E.[1]
		dry matter (g/m^2)		
774.6	710.9	781.8	636.1	21.14
		N g/m^2		
32.4	29.0	30.1	23.6	0.90

1 Standard error.

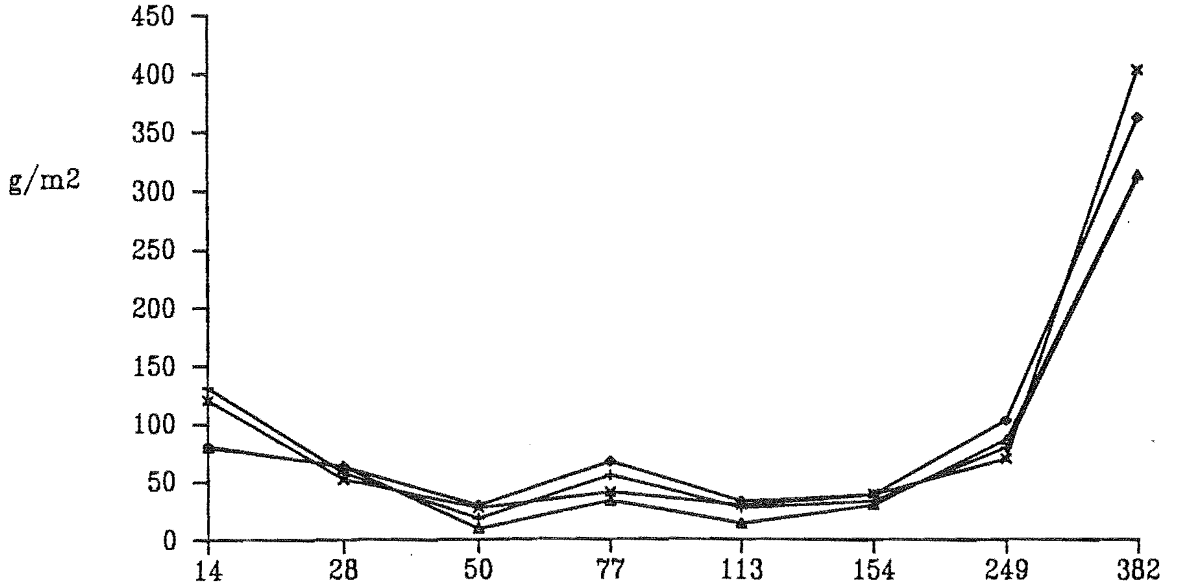


Figure 9.1 **Weight of dry matter removed from trenched and untrenched plots, September 1988-September 1989.**

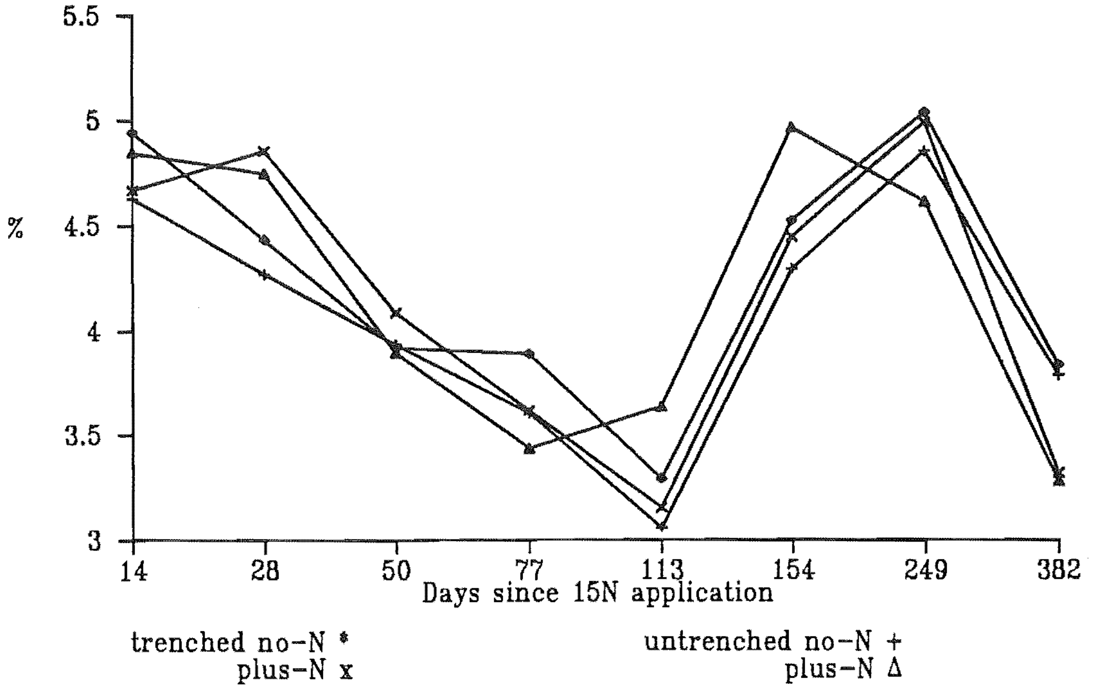


Figure 9.2 Nitrogen concentrations of pasture removed from trenched and untrenched plots, September 1988-September 1989.

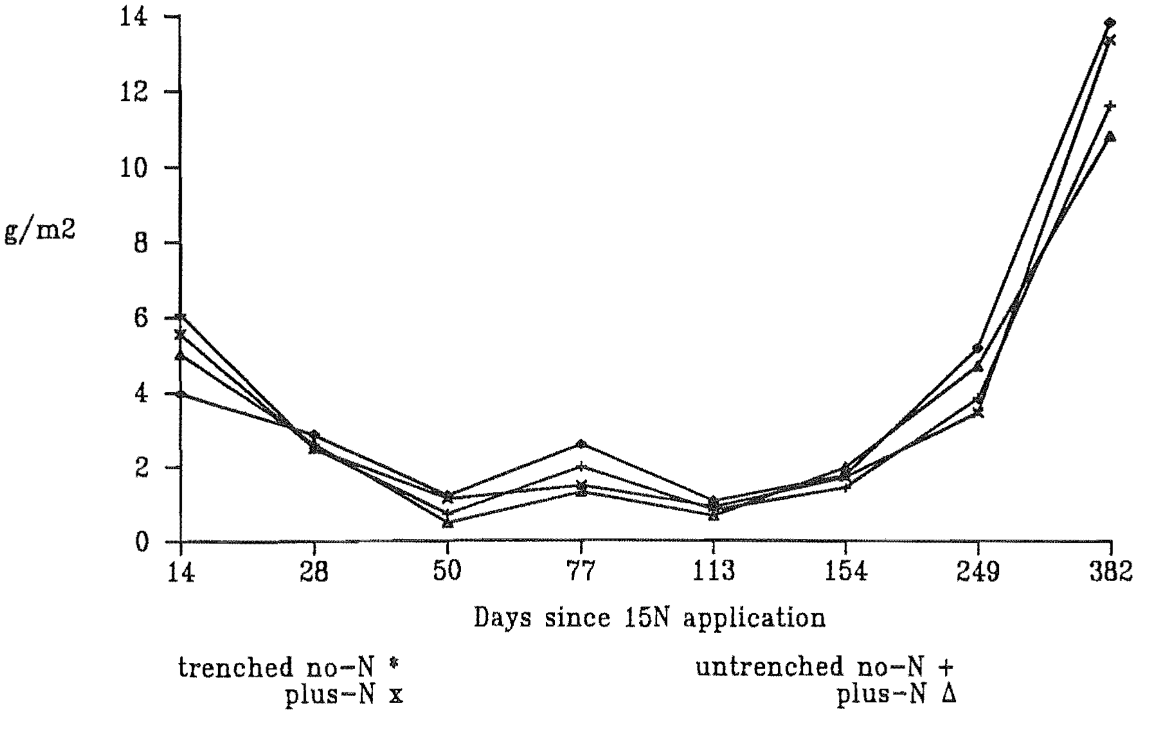


Figure 9.3 Weight of nitrogen removed in pasture clippings from trenched and untrenched plots, September 1988-September 1989.

Table 9.2 Total dry matter production for trenching and the main experiment, August 1988-May 1989.

	Plus-N	No-N	S.E.[1]
	g/m^2		
Trench	407	346	40.9
Main experiment	545	485	26.3

1 Standard error.

Table 9.3 Quantity nitrogen removed from trenching and the main experiments, August 1988-May 1989.

	Plus-N	No-N	S.E.[1]
	g/m^2		
Trench	18.0	15.4	17.72
Main experiment	25.6	20.3	13.06

1 Standard error.

The differences in the quantities of dry matter and N (Tables 9.2 and 9.3) removed in the trenching experiment and those in the main experiment may indicate subtle differences in microclimate between the different locations used in each experiment. The inherent variability in the system studied, however, was not addressed in this study.

9.3 Proportion of nitrogen derived from fertilizer in pasture and ^{15}N recovery in trenched and untrenched plots

Except for the first sampling date 14 days after ^{15}N application, %Ndff was consistently higher in pasture inside the trenched plots than in untrenched plots (Fig. 9.4), although this was not statistically significant (Appendix 9.3).

%Ndff was lower in the trenching experiment than in the main experiment on the recovery of $^{15}NH_4^+$ by pasture.

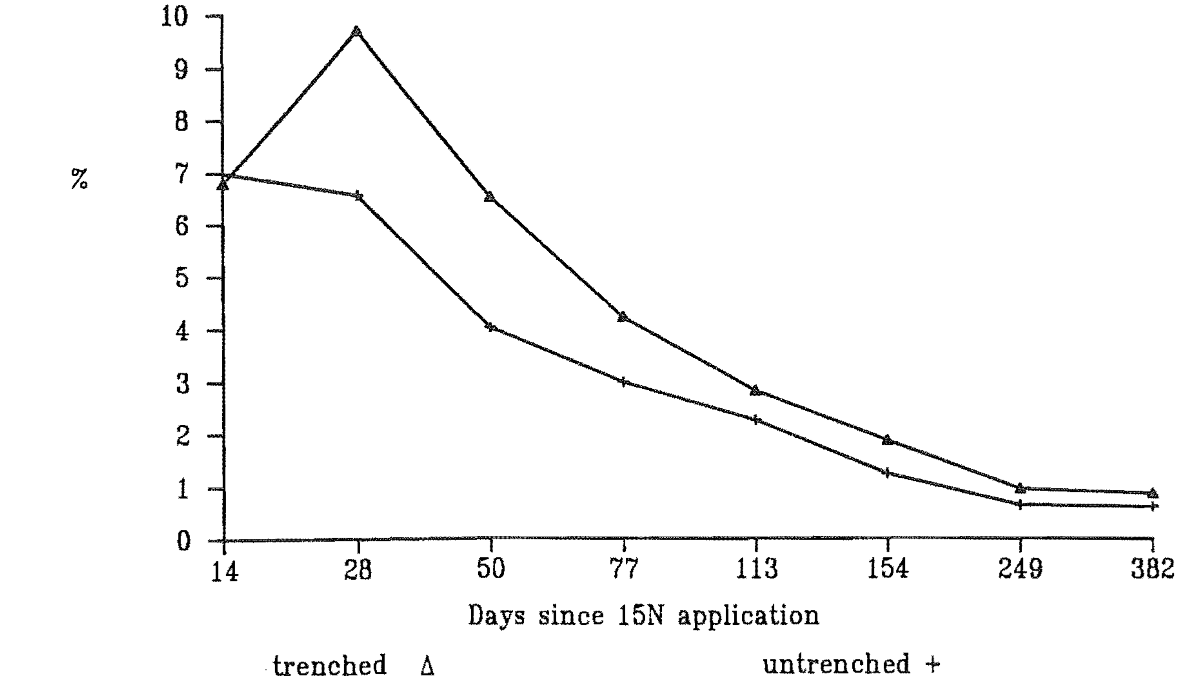


Figure 9.4 %Ndff in pasture clippings in trenched and untrenched plots (n = 3), September 1988-September 1989.

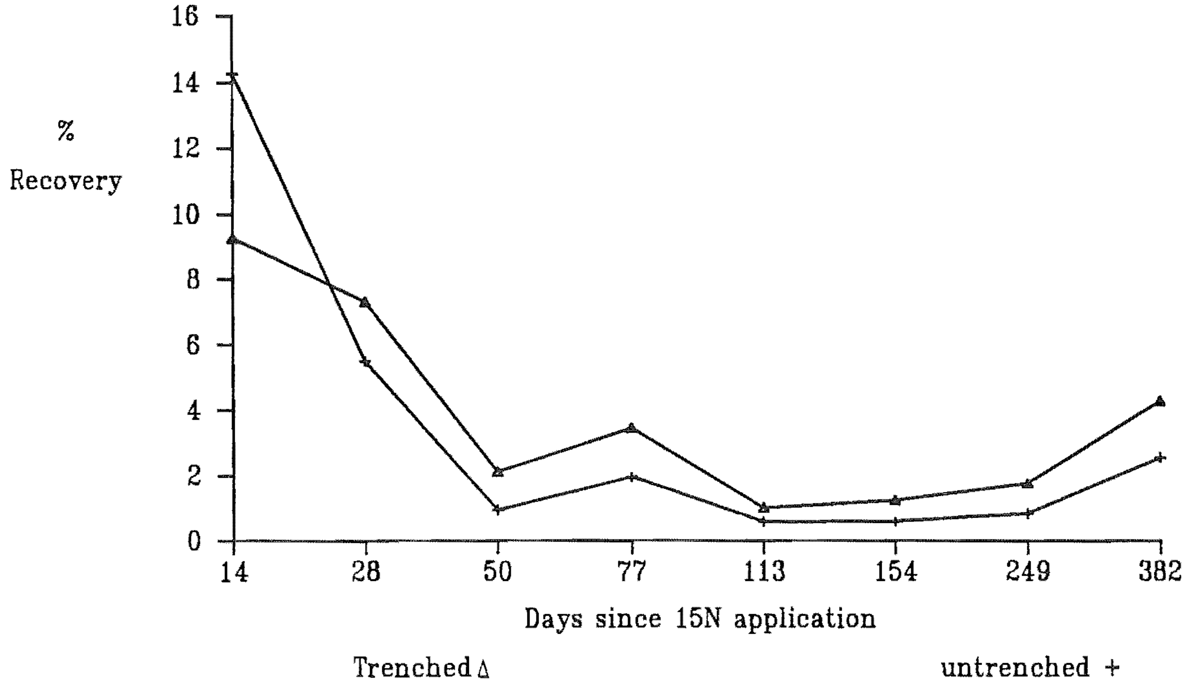


Figure 9.5 Percent ^{15}N recovery at each harvest in trenched and untrenched plots (n = 3), September 1988-September 1989.

At Day 14, approximately seven percent of N in the pasture in the trenched treatments was derived from the fertilizer and thereafter %Ndff declined slowly, except for an increase at Day 28. ^{15}N continued to remain available to the pasture but was taken up in decreasing proportions during the season.

The recovery of ^{15}N in the pasture showed similar trends and was not significant, except for differences between sampling dates (Fig. 9.5, Appendix 9.3). Except for at the first sampling, mean ^{15}N recovery was consistently higher in pasture clippings inside the trenched plots but overall there was no significant difference in the cumulative total of ^{15}N recovered in pasture from trenched or untrenched plots (Table 9.4).

Table 9.4 Percent ^{15}N recovery in pasture and soils of trenched and untrenched microplots.

	Trenched	Untrenched	S.E.[1]	P[2]
		%		
Herbage	30.4	27.2	4.199	0.5275
Soil	39.2	33.8	8.85	0.6077
Total recovery	69.6	61.0	13.04	0.5804

1 Standard error.
2 From paired T test that the mean of the differences is zero.

9.4 Retention of ^{15}N in soil

Retention of ^{15}N in soil in the trenched and untrenched plots was only assessed at the end of the experiment. There were no significant ($P < 0.05$) effects of trenching for total N concentration, atom $\%^{15}N$, %Ndff and total ^{15}N recovery in each of the soil horizons sampled 0-10 cm, 10-20 cm and 20-50 cm (Table 9.5). Trenching had no effect on total ^{15}N recovery in the top 50 cm of soil sampled. On average, 40% of the ^{15}N recovered in soils had been leached into the 20-50 cm depth of soil. Although not sampled, it is likely, given the wetter winter in 1989, that some ^{15}N was leached below 50 cm. Therefore, the recovery of ^{15}N in soil may be underestimated.

9.5 System recovery of ^{15}N

Recovery of ^{15}N in herbage and in the soil was summed for all trenched and untrenched plots (Appendix 9.4) and subjected to a paired T test (Table 9.4). There were no significant effects of trenching or monthly addition of N on either the herbage or the soil or their sum ($P < 0.05$). Overall, system recovery of ^{15}N was lower than in the main ^{15}N experiments but these differences are to be expected given the quite different nature of the two experiments. In the trenching experiment, ^{15}N was applied to unconfined microplots 0.36 m^2 and samples were collected from a central 0.25 m^2 plot whereas in the main experiment ^{15}N was applied to essentially discrete units containing a tree at their centre. There was little evidence in foliage samples from surrounding trees to suggest lateral movement of ^{15}N translocated in roots (Appendix 6.7). The open trenching experiment system obviously resulted in the loss of applied ^{15}N due to lateral movement of ^{15}N. Roots of pasture plants outside the microplots, but within the trenched area, may have removed ^{15}N.

Table 9.5 Summary of ANOVA of total nitrogen concentration, atom % ^{15}N, %Ndff and percent ^{15}N recovery in soils of trenched and untrenched plots.

Soil depth (cm)	Trenched	Untrenched	S.E.[1]	P[2]
		%N		
0-10	0.263	0.247	0.0124	0.4314
10-20	0.170	0.164	0.0044	0.3941
20-50	0.097	0.105	0.0124	0.6561
		atom %^{15}N		
0-10	0.378	0.377	0.0029	0.8654
10-20	0.372	0.373	0.0023	0.7790
20-50	0.375	0.373	0.0030	0.5886
		%Ndff		
0-10	0.171	0.158	0.0494	0.8650
10-20	0.075	0.092	0.0393	0.7794
20-50	0.127	0.084	0.0518	0.5919
		%^{15}N recovery		
0-10	17.3	14.7	5.20	0.7471
10-20	5.6	6.4	2.95	0.8547
20-50	16.3	12.7	6.94	0.7313

1 Standard error.
2 Probability of treatment differences according to ANOVA.

9.6 Summary

The results of the trenching experiment suggested that pine roots did not detrimentally affect ^{15}N uptake by pasture. This was probably due to the lack of pine roots in the untrenched plots at a distance of 2.5 m from the tree. This was confirmed by observations of declining pine root length with distance from the stem (P. Houston, 1989, unpub.), the lack of roots observed extending beyond 1.9 m when the trees were harvested, and the low %Ndff in needles of surrounding trees (Appendix 6.7).

Chapter Ten

Overview and discussion of results

10.1 *P. radiata* growth and biomass

The aim of this study was to examine the competitive mechanisms between *P. radiata* and pasture for N and soil moisture.

The height, diameter and biomass of *P. radiata* were greatly enhanced by the removal of pasture competition at age four years (Table 10.1). Tree height and root collar diameter growth were increased by the spraying treatment with root collar diameter showing a 22% increase compared with the plus-pasture treatments. Total tree biomass was increased 56% by removing pasture competition. Similar responses have been reported with the removal of weed competition during the establishment phase of *P. radiata* (Squire, 1977; Cellier and Stephens, 1980; Nambiar and Zed, 1980; Sands and Nambiar, 1984; West, 1984; Balneaves, 1987; Smethurst and Nambiar, 1989), but there are no known reports of weed control in established stands of *P. radiata*.

Table 10.1 Summary of tree height, root collar diameter and final tree biomass at age five, adjusted for initial differences in tree size.

Grazing		Rank		Spray	
Plus-N	No-N	Plus-N	No-N	Plus-N	No-N
		Height (cm)			
474	451	448	450	474	514
		Root collar diameter (cm)			
14.0	13.4	13.9	13.7	17.2	16.5
		Aboveground tree biomass (kg/tree)			
28.3	26.9	29.1	26.4	42.8	43.4
		Belowground tree biomass (kg/tree)			
5.1	5.7	6.5	5.4	9.0	8.8
		Total tree biomass (kg/tree)			
33.4	32.6	35.6	31.8	51.8	52.2

The addition of 30 kg N /ha each month did not result in greater tree growth. Responses to N are known to be variable depending on weed control and site condition (Ballard, 1984). For example, Squire (1977), Smethurst and Nambiar (1989), Thomas (1987, unpub.) have all reported responses in young *P. radiata*, whereas West (1984) found no effects. There have also been reports of undesirable side effects, for example, stem deformity (Smethurst and Nambiar, 1989; Swindel *et al.*, 1988) and insect attacks (Swindel *et al.*, 1988), although there were no such problems in this current experiment.

The lack of response to N by the trees in the pasture treatments in this study may be attributable to low soil moisture as a result of spring drought. In the sprayed treatments the release of N from sprayed pasture, especially from roots, and the mineralization of native soil N resulted in large amounts of available N. This may have reduced the growth response of trees to added N (McKee and Wilhite, 1988), a possibility raised by the increased N content in the sprayed-plus-N treatment due to the luxury uptake of N.

In terms of biomass production, removal of pasture competition almost doubled the weight of current needles, wood and branches. Even so trees in the plus-pasture treatment were heavier than other reports for the Canterbury region; this reflects differences in stocking and fertility. However, the trees in this study were of a comparable weight to those in trials with similar stocking in the Tikitere agroforestry study reported by Madgwick *et al.* (1983, unpub.) when allowances for age differences are made (Table 10.2).

The removal of pasture competition did not alter the pattern of photosynthate allocation between roots and shoots, although the root systems of trees in the no-pasture treatments were larger than those in the plus-pasture treatments.

In this study pine fine roots were sampled to a radius of 1.9 m around the sample tree. Very few roots were observed extending beyond this distance and only in the case of the largest tree in the spray-plus-N treatment did root systems of neighbouring trees overlap. Further, ^{15}N enrichments in neighbouring trees and the data from the trenching experiment suggested that root systems of neighbouring trees did not overlap. The sampled area constituted only 45% of the total area available to the trees and indicated that, at 400 stems per hectare, *P. radiata* was not fully utilizing the site. This is in contrast to higher stockings. For example Nambiar (1983) reported that for two to three-year-old *P. radiata* at 1890 stems per hectare growing on sandy soil, fine root distribution was independent of distance from the stem.

Table 10.2 Comparative data for aboveground biomass and nitrogen content of *P. radiata*.

Site	Age	Treatment	Height (m)	Stocking (stems/ha)	Aboveground biomass (kg/tree)	N content (g/tree)	N use efficiency[1]	Reference
Rangiora, New Zealand	5 years	pasture	4.55	400	27.67	203.8	135	This study (adjusted data)
		no-pasture	4.93		43.10	360.0	119	
		plus N	4.64		32.23	277.2	116	
		no N	4.71		33.38	234.4	142	
Mt Gambier, Australia	20 months	control	1.22	1587	0.29	1.9	152	Smethurst & Nambiar 1989
		stripweed control	1.58		0.83	5.5	156	
		total weed control	1.76		1.52	9.8	155	
		total weed control + 100 kg N/ha	1.81		1.81	17.6	102	
Bottle Lake plantation, New Zealand	2 years	control	1.60	2250	0.90	11.2	80	Thomas 1987, unpub.
	3 years	control	3.15		5.88	49.3	119	
	3 years	90 g N/tree	3.29		6.99	55.3	126	
Eyrewell, New Zealand	7 years	-	5.30	1540	15.11			Mead *et al.* 1984
Eyrewell, New Zealand	4 years	-	2.22	1200	2.35			Grottker 1984, unpub.
Tikitere, New Zealand	6 years	-	8.70	300	57.66	254.7	226	Madgwick *et al.* 1983 unpub.
	6 years	-	8.80	600	52.63	247.3	212	
Kaingaroa, New Zealand	2 years	-	1.05	2496	0.28	2.8	100	Madgwick *et al.*, 1977[2]
	4 years	-	3.91	2347	9.44	55.8	169	
	6 years	-	7.12	2224	23.56	93.5	251	

Table 10.2 continued

Puruki, New Zealand	4 years	-	4.00	1960	12.04	87.2	138	Beets & Pollock 1987a[3]
	5 years	-	5.75	1960	22.34	143.3	155	
	4 years	-	3.75	1843	7.05	51.2	137	
	5 years	-	5.00	1843	17.74	111.0	159	
	4 years	-	2.75	1969	4.57	34.1	134	
	5 years	-	4.50	1969	14.57	88.4	164	
Mt Gambier, Australia	3 years	35 g N/tree	3.34	5800	9.46	54.5	173	Fife & Nambiar 1982
Spehrs Plantation, Australia	4 years	control	3.89	1250	6.12			Nambiar & Fife 1987
	4 years	80 g N/tree	4.47	1250	12.89			
Belanglo, Australia	4 years	0	1.21		0.22			Snowdon & Waring 1985
	4 years	26 g N + 11 g P/tree	2.22	14233	1.04			
Billapaloola Plantation, Australia	3 years	-	1.4	1483	0.77			Forrest & Ovington 1970
	5 years	-	3.1	1492	3.56			
Mt Burr, Australia	5 years	4/18 g N/tree (no weeds)	8.0	1890	37.23	124.5	299	Nambiar & Bowen 1986

1 Index of N use efficiency calculated as units of aboveground biomass per unit of N in aboveground biomass.
2 Biomass data are found in Madgwick *et al.* 1977 whilst N content data are found in Madgwick 1985.
3 Biomass data are found in Beets and Pollock 1987a whilst N content data are found in Beets and Pollock 1987b.

Although aboveground biomass estimates were within the range reported elsewhere (Table 10.2), the estimate of fine root biomass less than one millimetre in diameter in all treatments was lower than in reports for *P. radiata* (Clinton, 1986, unpub.; Santantonio and Santantonio, 1987; Thomas, 1987, unpub.). Differences between studies of age, stocking, site fertility, methodologies and classification tend to confuse comparisons.

The drought conditions experienced during this study also influenced the dynamics of pine fine root biomass (Houston, 1989, unpub.). A significant gradient in pine root length was observed with root length decreasing with increasing distance from the stem in the rank-no-N and spray-no-N treatments (Houston, 1989, unpub.). Houston was also able to demonstrate an interaction between distance from stem and aspect. There were fewer fine roots less than one millimetre diameter at 1.53 m distance on the drier northern side of trees. There was also a slight, but non significant, decrease in the length of fine roots less than one millimetre diameter between the spring and summer samplings.

10.2 Pasture production

Pasture production estimates reported in this study were lower than some estimates for the Canterbury region although production is known to be affected by rainfall and summer drought (Hoglund, 1985). Hoglund found that in a high rainfall year (1003 mm) pasture production was 10,200 kg/ha but below average rainfall (502 mm) reduced pasture production by 26% to 7500 kg/ha (summer rainfall of 440 mm). The area-weighted estimate for the simulated-grazing treatment of 4393 and 3906 kg/ha for the plus-N and no-N treatments, respectively, for the period August 1988 to May 1989 with a summer rainfall of 267 mm, could well be within the normal range for Canterbury under conditions of low rainfall.

There was no difference in pasture root biomass between pasture treatments although it tended to be higher in the rank than in the simulated-grazing treatments. This could reflect the effects of the simulated-grazing treatment on pasture root biomass: repeated defoliation and reductions in root growth (Ennik and Baan Hoffman, 1983). This effect may have reduced pasture root length density in the simulated-grazing treatment and consequently reduced its competitive ability compared with rank pasture.

The positive effects of trees as shelter (Radcliffe, 1985) and of young trees on pasture growth (Cossens, 1984; Percival and Knowles, 1988) have been reported. In this study it was found that pasture growth in the rooting zone of the trees was 38% less on average than midway between trees. In this study there was also a pronounced visual rainshadow effect on pasture growth, although this was not quantified (Fig. 8.5).

The respective timing of pasture and tree growth were important. Pasture production declined rapidly with the onset of drought conditions during September and October. In contrast, tree height growth was rapid during September and

October and the foliage mass continued to develop until February, well after pasture production had been severely reduced by drought. Differences between treatments in needle weight became apparent during November. It is possible that this was associated with a drying out of deeper soil horizons closer to the trees, especially in the plus-pasture treatments.

The removal of pasture competition resulted in more water being available to trees; such trees responded favourably by continuing to grow longer into the summer compared with trees in the plus-pasture treatments which were affected by drier soils earlier.

10.3 Tree and pasture nitrogen uptake

Uptake and accumulation of N in the trees was increased by the removal of pasture competition; a similar response was reported by Smethurst and Nambiar (1989) for *P. radiata* due to weed control in plantations on sandy soils in South Australia. However, in this current study the monthly addition of N did not increase aboveground N content. In contrast, belowground N content was increased by both the removal of pasture competition and monthly addition of N.

Thomas (1987, unpub.) observed similar responses to N in aboveground and belowground N content of young *P. radiata*. It appears that one of the first effects of N fertilization is to increase belowground N content before there is a response aboveground. The size of the response may depend on the tree size and may take more than one growing season to appear.

The large increase in N content of sprayed trees, including the root systems, raises the question of how this increase came about. Firstly, it was found that soil mineral N concentrations and pools were higher in soils beneath trees of the sprayed treatments. This was due to there being no further uptake of N by pasture and perhaps the release of N from decaying pasture. Secondly, the death of pasture roots beneath trees following the spraying treatment could have released up to 72 g of N, in the 1.9 m radius plot beneath the tree, which is equivalent to 42% of N taken up by the trees in the sprayed treatments during this study. Once trees had access to this N pool and also to increased soil moisture, they may have been in a position to explore a larger soil volume more effectively.

This explanation is supported by the observation that a larger proportion of fine root biomass was in the 0-10 cm soil depth in the plus-pasture treatments than in the sprayed treatments. This observation reflects competition between trees and pasture for nutrients and water in the surface soils and suggests that a change in pine root distribution occurred when pasture competition was removed and trees were then able to exploit a larger soil volume.

Overall the spraying treatments increased N uptake into tree roots and shoots by 78%. The monthly addition of N did not increase uptake further; perhaps trees of this size were unable to take up more N than that already provided by the spraying treatment. Alternatively, to take full advantage of increased N supply *P. radiata* may need a good supply of moisture (Linder *et al.*, 1987). Lastly, the lack of N response may be due to an induced nutrient deficiency brought about by dry top soils and the deep-rooted nature of *P. radiata* that enables it to get moisture from deeper soil horizons which are low in available nutrients (Will, 1966; Will and Stone, 1967). This factor has not been tested experimentally for *P. radiata* but has been demonstrated for pasture species (Garwood and Williams, 1967).

In plantations, responses of weeds to applied fertilizers are common (Squire, 1977; West, 1984). Responses in pastures are also common (During, 1984), and have been observed when N fertilizers have been applied to pasture under *P. radiata* (Steele and Percival, 1984). In this study, N content of aboveground pasture responded to both the monthly addition of N and the simulated-grazing treatment (Fig. 10.1). Aboveground uptake of N was particularly marked when the N content of clippings in the simulated-grazing treatment was included. Rank pasture had more N in the stubble and roots than similar components in the simulated-grazing treatments: a consequence of greater root biomass in the rank treatment. Again this has an impact on the competition between trees and pasture for N.

In the rank treatment it is possible to compare pasture responses to applied N close to the tree (1.9 m radius) and midway between trees. The biggest response occurred midway between the trees where there was an 88% increase compared with an 18% increase within a 1.9 m radius of the trees.

Most N uptake into trees and pasture, when combined, occurred in the simulated-grazing treatments with the least total N uptake occurring in the sprayed treatments (Fig. 10.1). This may be compared with the size of the pool of net mineral N available in the soil at the end of the experiment. There were considerable quantities of residual mineral N in soils in all the plus-N treatments. The no-pasture and simulated-grazing treatments both had higher residual mineral N pools than the rank treatment, but it should be recalled that more N was applied to the simulated grazing-treatment compared with the other two. Even at the end of the experiment there was still residual mineral N in the soil of the spray-no-N treatment which contrasts with the rank-no-N treatment where there was no mineral N left at the end of the experiment. There was also some residual mineral N in the simulated-grazing-no-N treatment (Fig. 10.1). This was probably due to the application of N to simulate the return of N by grazing animals.

These differences in residual mineral N pool sizes are consistent with the growth and N uptake responses observed. Thus, there was a big pasture response to N in the rank treatment and the trees in that treatment were under the greatest N stress (Figures 5.3a and 5.3b). The lack of growth response to added N in trees in the sprayed treatment and the high level of residual mineral N supports the concept that the spraying treatment alone increased N supply substantially by removing pasture competition for N and releasing a large pool of available N.

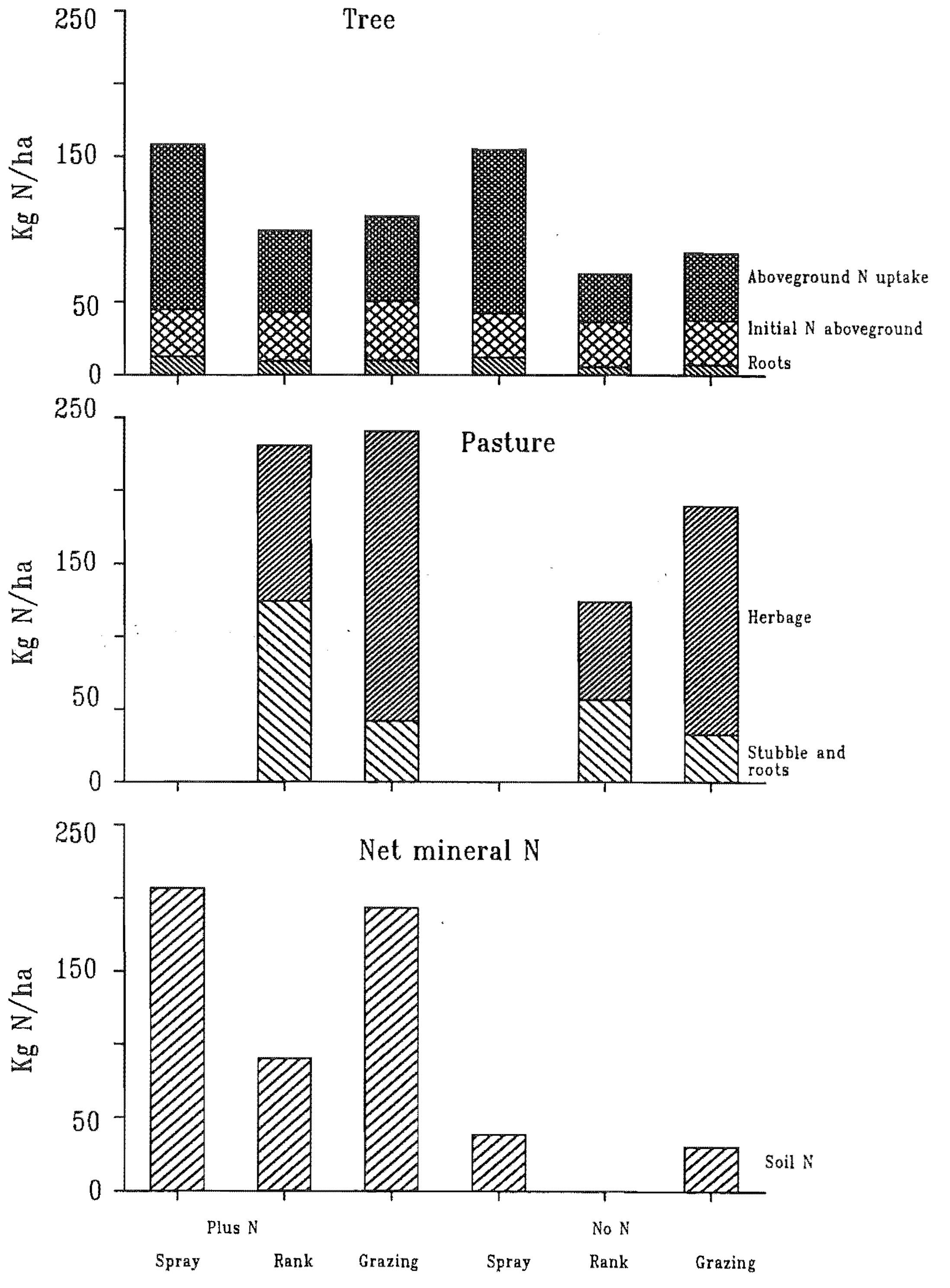


Figure 10.1 **Distribution of nitrogen in the pasture, trees and mineral nitrogen pool at the final harvest as influenced by nitrogen fertilizer and pasture management. The simulated-grazing pasture total includes removals during the course of the experiment and all pasture data are area weighted.**

Biomass and N content data can be integrated by calculating indices of N use efficiencies (Vitousek, 1982; Agren, 1983; Birk and Vitousek, 1986). In this study three indices of N use efficiency were calculated: two using accumulated standing crops of biomass and N, and one using increment in aboveground biomass and N.

There was a significant interaction between the level of pasture management and the addition of N for the quantity of biomass accumulated per unit of N in the aboveground biomass of *P. radiata* (Table 10.3, Appendix 10.1).

Efficiency of biomass production per unit of N was higher in the pasture treatments without added N. However, caution is required when interpreting these ratios in that they may reflect a temporary storage of N which may result in faster subsequent growth.

The quantity of biomass accumulated per unit of N in the aboveground biomass of *P. radiata* decreased in both the simulated-grazing and rank treatments as aboveground pasture biomass increased (Fig. 10.2). The effect of the simulated-grazing treatment was both to increase pasture production and also to decrease the amount of biomass accumulated per unit of N in aboveground biomass of *P. radiata*.

Alternatively, it may be more satisfactory to examine the notion of N use efficiency using a measure of the quantity of wood produced per unit of foliage N (Table 10.4, Appendix 10.2). The interaction between level of pasture competition and applied N was significant at $P = 0.0580$ and may have been more pronounced if the errors involved in measuring wood increment were lower. The results suggest that spraying reduced the N use efficiency; efficiency in simulated-grazing treatments was similar with and without N and was higher than in the sprayed treatment. The application of N to the rank treatment decreased N use efficiency substantially, presumably because moisture stress prevented response to N (see also Fig. 5.3b).

Table 10.3 Quantity of aboveground biomass per unit of nitrogen content for *P. radiata*, adjusted for differences in initial tree size using initial root collar diameter[2].

Grazing		Rank		Spray		
Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
			g dry matter/g N			
117	142	128	159	116	121	4.10

1 Standard error.

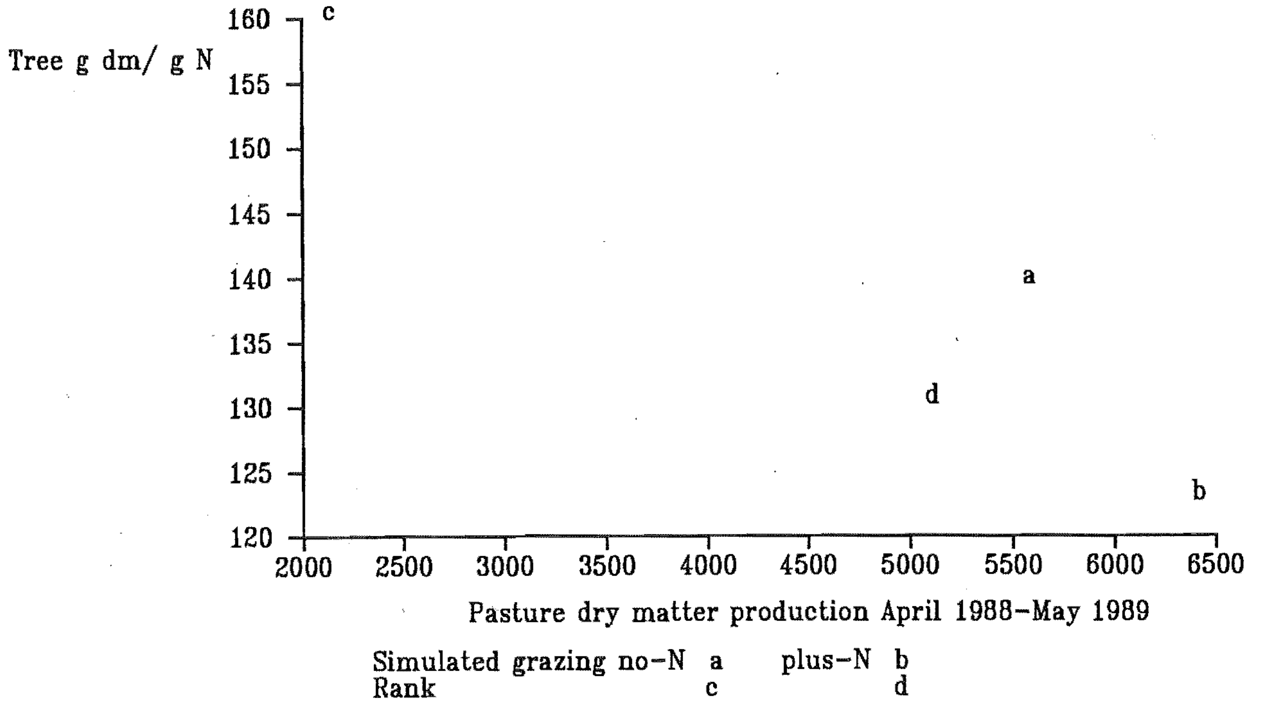


Figure 10.2 **The relationship between the ratio of aboveground biomass:aboveground nitrogen content of *P. radiata*, and the amount of pasture production.**

Table 10.4 **Ratio of current wood weight:total needle nitrogen weight - a measure of the efficiency of foliage nitrogen of *P. radiata*.**

Grazing		Rank		Spray		
Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
27.3	29.9	21.6	32.6	25.7	23.8	2.52

1 Standard error.

A third option is to use increments in aboveground biomass and N content. No significant treatment effects were apparent (Table 10.5, Appendix 10.3). This suggests that although the total quantities of biomass and N increment may differ between treatments the quantity of biomass increment per unit of N increment does not differ and there is no difference in N use efficiency between treatments. Biomass increment per unit of N taken up by *P. radiata* was on average 4.8 times greater than that of pasture.

Table 10.5 **Ratio of increment in aboveground biomass:increment of aboveground nitrogen content of *P. radiata* adjusted for differences in initial tree size using initial root collar diameter^2.**

Grazing		Rank		Spray		
Plus-N	No-N	Plus-N	No-N	Plus-N	No-N	S.E.[1]
136	132	135	125	138	133	5.15

1 Standard error.

The assessment of nitrogen use efficiency based on increment data provides the most utility when suitable information is available. Simple ratios of dry matter and nitrogen accumulated can be misleading, as by themselves they are nit a good direct estimate of nitrogen use efficiency with regards to productivity. Such efficiencies can be high due to retention of foliage N for many years, and also there can be large accumulations of biomass on poorer sites due to retention of foliage and also investment in root systems.

It was not possible to calculate a water use efficiency for *P. radiata*. Changes in soil moisture storage were similar for all treatments (Table 8.5) but given that in plus-pasture treatments this change was the sum effect of pasture-plus-tree removal, trees in these treatments probably used less water than those where the pasture had been removed.

10.4 Dynamics and recovery of ^{15}N

10.4.1 Immobilization of ^{15}N

Fourteen days after ^{15}N application considerable quantities of ^{15}N had been immobilized in the soil in all treatments except the sprayed treatment where recovery in the mineral N pool was higher than in the soil organic pool (Sections 4.2.2 and 4.2.5). Immobilization of $^{15}NH_4^+$ was rapid and in the simulated-grazing treatment 14 days after ^{15}N application 65% of the total $^{15}NH_4^+$ in soil was immobilized. This compares to only 49% for $^{15}NO_3^-$. There was also evidence that some of this immobilized $^{15}NO_3^-$ had subsequently been mineralized. This immobilization occurred even though treatments had received 155 kg N/ha prior to the 30 kg of ^{15}N-labelled fertilizer being applied. However, the pool of plant-available mineral N was small in these treatments, on average 24 kg/ha.

The quantity of ^{15}N immobilized by Day 14 is of a similar proportion to the total amount of N immobilized within a similar time frame for several agricultural and forestry studies even though the quantity of ^{15}N applied here was smaller than in most studies (Mead and Pritchett, 1975a; Heilman *et al.*, 1982a; Bristow *et al.*, 1987; Thomas, 1987, unpub.; Melin and Nommik, 1988; Ledgard *et al.*, 1988).

When pasture was not present $^{15}NO_3^-$ accumulated in the soil suggesting that either pasture removal promoted nitrification due to increased NH_4^+ supply or perhaps any NO_3^- produced was rapidly utilized by pasture because in the plus-pasture treatments levels of $^{15}NO_3^-$ were low except where $^{15}NO_3^-$ was applied.

Even though immobilization of ^{15}N in the sprayed treatment was initially a lot lower than in other treatments, the difference only resulted in a doubling of tree ^{15}N recovery. It would appear that the trees were not in a position to utilize the quantity of available ^{15}N. This may be due to the low root length density of *P. radiata*. It is also possible that they had already taken up large quantities of N before the ^{15}N application, thus reducing their immediate need.

Although immobilization was greater in the plus-pasture treatments, uptake of ^{15}N in the simulated-grazing treatment that received $^{15}NH_4^+$ was 13% of the total applied, whilst 23% of the total $^{15}NO_3^-$ applied was recovered in the clippings in the first harvest. As well, considerable ^{15}N may have been contained in the stubble and root systems of the pasture (Bristow *et al.*, 1987), but this was not sampled. Bristow *et al.* (1987) report 23 and 13% recovery in stubble and roots, respectively, some 10 days after ^{15}N application. This represented 41% of total system recovery at that point. Furthermore, the dry conditions at this time were not conducive to pasture growth and may have limited pasture uptake of ^{15}N. It is also possible that pasture uptake may have been reduced due to N fixation by clovers.

Whatever the limitations to pasture ^{15}N uptake were, the study of tree and pasture ^{15}N uptake suggested that pasture was able to take up a lot more ^{15}N than trees during a period when immobilization was occurring. It is considered that this was due to the much higher root length density of pasture species compared with that of the trees.

In this current study the pattern of decreasing ^{15}N-labelled KCl-extractable mineral N is similar to that reported in other studies (Heilman *et al.*, 1982a; Bristow *et al.*, 1987; Ledgard *et al.*, 1988; Melin and Nommik, 1988; Preston *et al.*, 1990; Whitehead and Bristow, 1990) although residual levels tended to be higher. For example, Heilman *et al.* (1982a) found that nine days after ^{15}N application, recovery of KCl-extractable mineral N ranged from 15 to 134% but had declined to a range of 4-11% after 24 weeks. Quantities of soil mineral N had dropped from around 120-218 kg N/ha to 13-43 kg N/ha. In this study, 22 weeks after N application, recovery was between 9.8 and 25.6% depending on treatment. However, total mineral N had increased from 18-70 to 112-218 kg N/ha as a result of the continued monthly applications and the return of some N removed in clippings.

Immobilization of ^{15}N in soils of the sprayed plots may have occurred rapidly after Day 14. By Day 154, 52% of soil ^{15}N was in the organic form. As well total recovery in soil had declined from 67 to 49%, a drop of nearly 20% in the soil pool of ^{15}N. The high recovery of ^{15}N in the soil mineral N pool at Days 154 and 249 was due to $^{15}NO_3^-$ remaining available longer in this form because it is not readily immobilized. This observation was especially apparent in the $^{15}NO_3^-$-treated simulated-grazing and $^{15}NH_4^+$-treated spray treatments; considerable nitrification had occurred in the latter. Plant uptake and recovery of ^{15}N was likely reduced by drought. The increased availability of $^{15}NO_3^-$ was also observed for $NH_4{}^{15}NO_3$ fertilizer by Preston *et al.* (1990) in acid forest soils.

In this study it was shown that the pool of ^{15}N in soil remained relatively constant between 14 and 249 days following application, especially in the plus-pasture treatments. The stable pool of ^{15}N in soil occurred even though uptake by both trees and pasture was occurring and, after Day 14, was considerable in the plus-pasture treatments. It is unlikely that errors associated with soil sampling would mask this uptake. Several components of the system studied may have offered storage sites for ^{15}N. ^{15}N removed in clipped pasture may have come from that stored in pasture stubble and roots (Bristow *et al.*, 1987). ^{15}N may also have been stored in tree tissues that were not sampled during the experiment. The soil ^{15}N pool may further have been maintained by the ^{15}N released following the death of pasture and tree roots due to the drought conditions.

There is some evidence to suggest that ^{15}N uptake from soils had resumed by the time of the final harvest. The %Ndff in fine root systems, especially pine fine roots less than 1 mm diameter, was higher than in aboveground tissues. Similarly, %Ndff in pasture roots and stubble was higher than in new pasture growth in the simulated-grazing treatment.

10.4.2 Litter ^{15}N recovery

The high recovery of ^{15}N in the litter component of the rank plots at the final harvests suggests that although ^{15}N recovery in living herbage was low, it is highly probable that ^{15}N recovery in herbage had been higher earlier on. If this was the case, the assessment of ^{15}N recovery in rank pasture at the end of the experiment is only an assessment of the net competitive effect of rank pasture on *P. radiata* uptake given that there was death and decay of rank herbage before the final assessment. Cycling of ^{15}N very likely occurred in rank pasture due to death and decay. Ideally subplots within the rank treatment plots should have been successively harvested in order to follow N uptake.

Less ^{15}N was retained in litter of the sprayed treatment than in the plus-pasture treatments. Although this was not a large amount it points to an important difference between the plus-pasture and sprayed treatments. This process may reduce the loss of ^{15}N (Vitousek and Matson, 1984), and may also act as a source of ^{15}N for future plant uptake.

The simulated-grazing treatment also reduced litter ^{15}N recovery compared with the rank treatment. This was probably due to the non replacement of ^{15}N removed in the clippings.

10.4.3 ^{15}N uptake by trees

The ^{15}N isotope has been used as a tracer in studies of competition between plants (Bjorkman and Lundeberg, 1971; Atkinson, 1977; Ismaili and Weaver, 1986; Marion *et al.*, 1987), and plants and microbes (Jackson *et al.*, 1989) but rarely have complete recovery budgets been presented.

On average, %Ndff in *P. radiata* biomass components was higher in those trees treated with $^{15}NO_3^-$ than in $^{15}NH_4^+$-treated trees. However, this difference does not conclusively suggest a preference for N in the NO_3^- form. It is more likely that this was due to the increased availability of $^{15}NO_3^-$ in the soil compared to the $^{15}NH_4^+$. Although more $^{15}NO_3^-$ was taken up than $^{15}NH_4^+$, the quantities were not significantly different. This result does not resolve the question of whether *P. radiata* or other conifers prefer NO_3^- or NH_4^+, but it does suggest that the outcome of experiments with small seedlings (Mcfee and Stone, 1968; Flewelling, 1979; Skinner, pers. comm.) may not translate very well to young trees during a phase of rapid growth when plant N requirements are high and N supply is limited.

The range of tree recoveries of applied ^{15}N for this study are within the range reported previously for *P. radiata* (Thomas, 1987, unpub.; Nambiar and Bowen, 1988) and also for a wide range of conifer and experimental field situations (Table 10.6). Much higher recoveries have been reported (Table 10.7) but only for pot trials (Pang, 1985) and sometimes for $^{15}NO_3^-$-type fertilizers, or reports are based on indirect measurements (Steele and Percival, 1984; Raison *et al.*, 1990).

It appears that rate and method of application, and tree age do not greatly affect ^{15}N uptake by *P. radiata* once the reports of Steele and Percival (1984) and Raison *et al.* (1990) have been investigated. In the unreplicated study of Steele and Percival (1984) tree ^{15}N uptake was not measured quantitatively and was obtained by the difference between the total applied and that recovered in pasture and soils after 84 days. The high recovery of N fertilizer measured by Raison *et al.* (1990) using indirect methods did not allow for retranslocation, the uptake of native soil N and assumed all N was taken up from fertilizer.

In the study reported here ^{15}N was applied in spring at a time of rapid growth and good recovery was achieved by the pasture. Nevertheless, uptake by the trees in all treatments was relatively low. This low uptake was unlikely to be due to the time of application. Thomas (1987, unpub.) found no difference between autumn, spring and summer applications and recovery was not affected by splitting fertilizer applications. Whilst the uptake of ^{15}N by *P. radiata* increased from 8.0 to 15.4% when pasture competition was removed, the increase, although large in relative terms (92%), did not represent a very large proportion of the total applied. It is probable that the ^{15}N uptake was still limited, despite removal of pasture competition, by the low root length density of trees and the immobilization of ^{15}N in the soils.

Table 10.6 Comparative data for percent recovery of applied ^{15}N-labelled fertilizer in forest ecosystems.

Species	Age (years)	Duration (months)	Bounded plots	Labelled fertilizer	Fertilizer rate (kg/ha)	Tree recovery	Other vegetation	Soil	Litter	Total	Reference
						%					
Scots pine	12	15	x	$(^{15}NH_4)_2SO_4$	50	5	NR[1]	NR	NR		Nommik 1966
				$Ca(^{15}NO_3)_2$	50	9	NR	NR	NR		Nommik 1966
Scots pine	15	5		$(^{15}NH_4)_2SO_4$	60	12.9	7.9	58.5	NR	79.3	Bjorkman *et al.* 1967
				$Ca(^{15}NO_3)_2$	60	11.7	21.6	56.3	NR	89.6	Bjorkman *et al.* 1967
Scots pine	80	12		$CO(^{15}NH_2)_2$	53	2.3	19.4	44	-	65.7	Paavilainen 1973
Scots pine	120-140	24		$^{15}NH_4NO_3$	100	22.7	7.5	51.9	NR	82.1	Melin *et al.* 1983
				$NH_4{}^{15}NO_3$	100	28.4	8.6	38.9	NR	75.9	Melin *et al.* 1983
Slash pine	13	24	x	$(^{15}NH_4)_2SO_4$	56	11	0.1	20.6	9.0	54.2	Mead & Pritchettb 1975
				$(^{15}NH_4)_2SO_4$	224	11	0	11.7	6.2	44.5	Mead & Pritchettb 1975
P. radiata	0.1	12		$(^{15}NH_4)_2SO_4$	8	6	Veg. sprayed	ND[2]	-		Nambiar & Bowen 1986
	1	12			34	18	Veg. sprayed	ND	-		Nambiar & Bowen 1986
Douglas fir	6	24		$CO(^{15}NH_2)_2$	224	30		38		68	Heilman *et al.* 1982b
Scots pine	29-43	24	x	[3]	40	38	NR	46		84	Nommik & Larsson 1989
					160	36	NR	12	12	60	Nommik & Larsson 1989
P. radiata	2	18		$CO(^{15}NH_2)_2$	50	21.3	Sprayed	69	NR	90.2	Thomas 1987, unpub.
				$CO(^{15}NH_2)_2$	150	21.5	Sprayed	53	NR	74.8	Thomas 1987, unpub.
Scots pine	50	24		$Ca(^{15}NO_3)_2$	150	44	1	31	NR	76	Melin & Nommik 1988
				$^{15}NH_4{}^{15}NO_3$	150	33	1	54	NR	88	Melin & Nommik 1988
				$^{15}NH_4NO_3$	150	31	1	60	NR	92	Melin & Nommik 1988
				$CO(^{15}NH_2)_2$	150	20	1	66	NR	87	Melin & Nommik 1988

Table 10.6 continued

Scots pine	50	2 years		$CO(^{15}NH_2)_2$	150	20	1	66		87	Melin 1986
	50			$^{15}NH_4{}^{15}NO_3$	150	33	1	54		88	Melin 1986
	50			$Ca^{15}NO_3$	150	44	1	31		76	Melin 1986
	50			$^{15}NH_4{}^{15}NO_3$	50	28	2	70		100	Melin 1986
	35			$^{15}NH_4{}^{15}NO_3$	150	45	1	28		73	Melin 1986
	120			$^{15}NH_4{}^{15}NO_3$	150	20	1	61		82	Melin 1986
Picea mariana	5-6	0.5	x	$(CO^{15}NH_2)_2$	56	8.2	-	-	-	-	Knowles & Lefebvre 1972
Loblolly pine				$(^{15}NH_4)_2SO_4$	[4]		11[5]	52	31	94	Vitousek & Matson 1984
					[6]		9	42	29	69	Vitousek & Matson 1984
					[7]		13	55	5	73	Vitousek & Matson 1984
					[8]		9	55	5	69	Vitousek & Matson 1984
Lodgepole pine	11	9	x	$CO(^{15}NH_2)_2$	100	10.1	2.4	61.6	-	74.1	Preston *et al., 1990*
				$^{15}NH_4NO_3$	100	5.3	2.9	73.0	-	81.2	Preston *et al., 1990*
				$NH_4{}^{15}NO_3$	*100*	*1.9*	*3.4*	*41.1*	-	*46.4*	*Preston et al., 1990*
Sitka spruce	20	16		$CO(^{15}NH_2)_2$	160	13.1	-	90	-	103	Hulm & Killham, 1990

1 Not reported.
2 Not done.
3 Average data for $Ca(^{15}NO_3)$, NH_4NO_3 and $CO(^{15}NH_2)_2$.
4 Chopped no herbicide.
5 Pooled vegetation.
6 Chopped plus herbicide.
7 Shearing, piling and discing no herbicide.
8 Shearing, piling and discing plus herbicide.

Table 10.7 ^{15}N recovery data from pot trials with tree species.

Species	Age (years)	Duration (months)	Fertilizer labelled	Rate (kg/ha)	Tree recovery	Soil	Total recovery	Reference
					%			
Picea mariana	5-6		$CO(^{15}NH_2)_2$	56	11.7			Knowles and Lefebvre 1972
Scots pine	1	12	$CO(^{15}NH_2)_2$	100	16	61	77	Huser 1971
			$(^{15}NH_4)_2SO_4$		22	63	85	Huser 1971
			$Ca^{15}NO_3)_2$		25	29	54	Huser 1971
Norway spruce	1	12	$CO(^{15}NH_2)_2$	100	5	70	75	Huser 1971
		24	$CO(^{15}NH_2)_2$		18	67	85	Huser 1971
		12	$(^{15}NH_4)_2SO_4$		7	71	78	Huser 1971
		24	$(^{15}NH_2)_2SO_4$		17	59	76	Huser 1971
		12	$Ca(^{15}NO_3)_2$		17	40	57	Huser 1971
		24	$Ca(^{15}NO_3)_2$		28	39	67	Huser 1971
Douglas fir	4	12	$CO(^{15}NH_2)_2$	200	40.7	45.4	86.1	Pang 1985
		24	$CO(^{15}NH_2)_2$		42.4	40.6	83.0	Pang 1985
		12	$^{15}NH_4NO_3$		38.9	48.2	87.1	Pang 1985
		24	$^{15}NH_4NO_3$		48.2	37.6	85.8	Pang 1985
		12	$NH_4{}^{15}NO_3$		59.9	21.4	81.3	Pang 1985
		24	$NH_4{}^{15}NO_3$		66.2	17.2	83.4	Pang 1985
Douglas fir	0.1	9	$CO(^{15}NH_2)_2$	224	23.64	76.80	100.77	Marshall & McMullen 1976

Thomas (1987, unpub.) suggested that tree root systems responded first to N fertilizer and were then able to explore a greater soil volume. This, however, does not necessarily lead to greater N recovery unless considerable mineralization of immobilized ^{15}N occurs. This has yet to be demonstrated for any tree species.

10.4.4 Recovery and system retention of ^{15}N

The influence of competing vegetation on tree uptake and on soil retention of ^{15}N have not been examined in the past although some studies report uptake by understorey vegetation. Melin *et al.* (1983) and Preston *et al.* (1990) both showed that ^{15}N uptake by understorey vegetation was between 3 and 13%. In the study of Melin *et al.* (1983), uptake by understorey vegetation was approximately half that of tree uptake, while Preston *et al.* (1990) report that understorey vegetation took up between one fifth and twice the amount of ^{15}N taken up by trees, depending on treatment.

The lowest reported uptake by understorey vegetation was 0.1% in a closed stand of slash pine (Mead and Pritchett, 1975b) and the highest was 21.6% in a young naturally regenerating stand of scots pine with a dense ground cover of *Calluna vulgaris* and *Vaccinium vitus idaea* (Bjorkman *et al.*, 1967) (Table 10.6); this compares with 41.0 and 15.6% for the simulated-grazing and rank pasture treatments, respectively, in this study.

Some studies have removed competing vegetation and subsequently applied ^{15}N-labelled fertilizers without a suitable control and hence there has been no quantification of the impact of competing vegetation on ^{15}N uptake and efficiency of ^{15}N use. It cannot be determined if significant increases in tree uptake occurred as a result of removing competing vegetation or if losses by leaching, volatilization and denitrification were enhanced. On the other hand, where Paavilainen (1973) had not removed the vegetation and recovery by this vegetation was high (19.4%), the ^{15}N uptake by trees was very low (2.3%). Vitousek and Matson (1984) did not report the effect of competing vegetation on tree ^{15}N uptake although combined uptake by trees plus other vegetation was only 20% higher than in the herbicide treatment.

The form of N ($^{15}NH_4^+$ or $^{15}NO_3^-$) may also affect the recovery under various weed control strategies although this was not assessed in this current study. The experimental designs in past studies do not allow definitive conclusions to be made about the effect of competition on tree uptake. However, their findings suggest that competition may be an important part of ecosystem dynamics. Contrasting treatments should be considered in all future forestry ecosystems where ^{15}N uptake, efficiency and retention are of interest. In this study competition for ^{15}N-labelled fertilizer and its retention were examined and quantified, and found to play an important role (Table 10.8).

Reserves of ^{15}N retained in competing vegetation may reduce initial loss of ^{15}N by leaching and may act as a source of ^{15}N slowly released to the tree (Vitousek and Matson, 1984). The importance of this source of ^{15}N may have more

Table 10.8 Recovery of ^{15}N in major ecosystem components.

	Grazing		Rank	Spray
	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$
	% ^{15}N recovery			
Tree				
Aboveground	9.0	7.2	5.3	14.3
Belowground	0.8	0.9	0.9	1.1
Total tree	**9.8**	**8.1**	**6.2**	**15.4**
Pasture				
Aboveground	42.5	30.4	7.5	0.2
Belowground	2.9	6.2	8.0	-
Total pasture	**45.4**	**36.6**	**15.5**	**0.2**
Litter	2.2	2.7	5.6	1.6
Soil 0-10 cm				
Inorganic	21.8	13.8	13.0	14.1
Organic	19.0	21.8	27.4	33.2
Soil 10-20 cm				
Organic	8.7	7.2	9.0	8.4
Total soil 0-20 cm	**49.5**	**42.8**	**49.4**	**55.7**
Total vegetation[1]	54.8	46.1	24.5	13.7
Surrounding trees	0.2	0.2	0.3	0.3
System total[1]	**106.6**	**91.6**	**75.8**	**71.0**

1 Total not additive because adjusted values for tree recoveries presented.

importance than the release of ^{15}N immobilized in soil as a long-term source of ^{15}N for trees. In support of this, Smethurst and Nambiar (1989) suggest that although weeds competed for N during establishment and early growth of *P. radiata*, weeds retained N on the sandy soils of their particular site and, upon canopy closure, this N would be slowly released. Other practical examples of N storage by vegetation include the release of N from marram grass growing under *P. radiata* (Mead and Gadgil, 1978), and growing legumes in forest plantations (Gadgil, 1983).

The role of vegetation in influencing N transformations has also been described by Vitousek and Matson (1984). They found that herbicide and intensive site preparation (shearing, piling and discing) treatments influenced N immobilization and mineralization. Furthermore, losses by leaching and denitrification were greatest where organic residues had been removed and competing vegetation eliminated with herbicides. Their incubation studies showed that organic residues were responsible for increased immobilization of ^{15}N.

In this study increased uptake of ^{15}N in the sprayed treatment appeared to occur because the ^{15}N applied as $^{15}NH_4^+$ persisted in the plant-available forms of mineral $^{15}NH_4^+$ and $^{15}NO_3^-$ for longer than in the pasture treatments. $^{15}NO_3^-$ also persisted longer in the $^{15}NO_3^-$-treated plots. There is little competition for NO_3^- in soils between the processes of plant uptake and immobilization of N (Jones and Richards, 1977). Thus, NO_3^- was more available than the rapidly immobilized $^{15}NH_4^+$.

After application $^{15}NH_4^+$ was rapidly transformed to $^{15}NO_3^-$ in the sprayed treatment and although this happened to a lesser extent in the $^{15}NH_4^+$-treated simulated-grazing and rank treatments it appears that either plant competition limited N transformations or that NO_3^- was rapidly taken up by either pasture or trees.

By mid to late summer (154 days after application) levels of ^{15}N-labelled mineral N had in general declined and relative uptake rates of ^{15}N into pine foliage had declined. Uptake of ^{15}N by pasture in the simulated-grazing treatment had also declined by this time and pasture in the rank treatment had started to die off.

^{15}N uptake in the simulated-grazing treatment is similar for other clipping studies of pasture where there has been no return of ^{15}N removed in clipped pasture. Recoveries have ranged from 14 to 92% in shoots plus roots for a range of fertilizer rates and study lengths (Table 10.9). In this current study the simulated-grazing treatment increased pasture $^{15}NH_4^+$ by 135% compared with the rank treatment.

In this current study there was no influence of competing pasture or its management on ^{15}N retention in soils; on average 49% of that applied was recovered in the top 20 cm of soil. This is lower than in some reports for forest soils (Table 10.6), but higher than some reports for pasture soils (Table 10.9). However, there are differences in soil types, study lengths and depths of sampling that complicate comparisons. In both forestry and pastoral studies ^{15}N retention in soils has been influenced by the form, timing and rate of application of ^{15}N.

In the simulated-grazing treatment total ecosystem recovery did not appear to be influenced by the form of ^{15}N-labelled N. However, total ecosystem recovery appeared to be influenced by competing vegetation and its management. Recovery in the rank and sprayed treatments was considerably lower than in the simulated-grazing treatments although there was no difference between treatments in the recovery of $^{15}NH_4^+$.

There is no obvious explanation for this loss of ^{15}N in the sprayed and rank treatment. Within the experimental error it was not possible to detect differences in the recovery of ^{15}N in soils at the end of the experiment. In the

Table 10.9 Comparative data for percent nitrogen recovery of applied ^{15}N-labelled fertilizer in pasture ecosystem studies (some field and pot trial results).

Timing	Duration (months)	Labelled fertilizer	Rate (kg/ha)	First harvest	Final harvest: Total aboveground	Final harvest: Roots	Final harvest: Soil	Final harvest: Total recovery	Reference
				%	%	%	%	%	
Autumn	6	$CO(^{15}NH_2)_2$	50	10.6 (55)[1]	26.6	4.4	27	58	Ledgard *et al.* 1988
Winter	5			16.1 (28)	44	3.0	23	70	Ledgard *et al.* 1988
Spring	3			44.6 (29)	59.5	3.5	36	99	Ledgard *et al.* 1988
Spring	18	$Ca(^{15}NO_3)_2$	193	63 (30)	73	19	15	107	Hansson & Petterson 1989
Late summer	<1	$(^{15}NH)_2SO_4$	300	5.0 (22)	-	2.3	80.5	87.8	Keeney & MacGregor 1978
		$CO(^{15}NH_2)_2$		10.1	-	3.8	80.0	93.8	Keeney & MacGregor 1978
		$K^{15}NO_3$		4.3	-	2.3	76.1	82.7	Keeney & MacGregor 1978
Pot trial	7 weeks	$^{15}NH_4{}^{15}NO_3$	90	53	-	25	17	95	Watson 1987
		$CO(^{15}NH_2)_2$		31	-	16	13	61	Watson 1987
Pot trial	3	$(^{15}NH_4)_2SO_4$		19.5 (42)	46.2	30.7	21.2	98.1	Ledgard *et al.* 1989
Spring	3	$CO(^{15}NH_2)_2$	25	37.6 (23)	61.2		31.9	93.1	Steele & Percival 1984
			50	37.6	53.4		30.0	83.4	Steele & Percival 1984
			100	32.1	48.5		25.4	73.9	Steele & Percival 1984
			25	39.1	49.4		18.0	67.4	[2] Steele & Percival 1984
			50	34.7	46.3		22.5	68.8	[2] Steele & Percival 1984
			100	33.5	41.5		20.0	61.5	[2] Steele & Percival 1984
			25	23.3	38.8		22.9	61.7	[3] Steele & Percival 1984
			50	20.9	31.6		23.4	55.0	[3] Steele & Percival 1984
			100	22.7	33.9		25.5	59.4	[3] Steele & Percival 1984

Table 10.9 continued

Spring	12	$^{15}NH_4{}^{15}NO_3$	60	32.7 (28)	55.9	6.6	19.1	81.6	Bristow *et al.* 1987
Spring	6	$^{15}NH_4{}^{15}NO_3$	130	45.3	52	7.3	13.8	74	[4] Whitehead & Dawson 1984
				49.69	53	7	12.6	75	[5] Whitehead & Dawson 1984
Spring	5	$(^{15}NH_4)_2SO_4/K^{15}NO_3$	120		61		19	80	[6] Chabrol *et al.* 1988
Spring	1 day	$(^{15}NH_4)_2SO_4$	-		8.7		67.7	76.4	[7] Jackson *et al.* 1989
		$K^{15}NO_3$	-		19.6		64.4	84.0	Jackson *et al.* 1989
Pot trial	3	$(^{15}NH_4)_2SO_4$	100 mg N/pot		50		27	77	Walker *et al.* 1956
		$K^{15}NO_3$	100 mg N/pot		43		21	63	Walker *et al.* 1956
		$(^{15}NH_4)_2SO_4$	200 mg N/pot		57		17	74	Walker *et al.* 1956
		$K^{15}NO_3$	200 mg N/pot		49		15	64	Walker *et al.* 1956
Summer	11	$CO(NH_2)_2$[8]	740	4.96 (16)	12.66	1.86	28	40.7	Whitehead & Bristow 1990
Lysimeters	12	$Ca(^{15}NO_3)_2$	400		43.54				Dowdell & Webster 1980
Lysimeters	5.7	$Ca(^{15}NO_3)_2$	400		59		32	91	Webster & Dowdell 1985
Lysimeters	12	$Ca(^{15}NO_3)_2$	200		65		NR[9]		Lindberg *et al.* 1989

1 Days since application.
2 Stocking of 200 stems/ha *P. radiata*.
3 Stocking of 400 stems/ha *P. radiata*.
4 Irrigated.
5 Unirrigated.
6 Maize.
7 Includes roots.
8 Labelled urine.
9 Not reported.

sprayed treatment the loss of ^{15}N was not balanced by tree uptake, rather it occurred mainly from the ^{15}N-labelled mineral N pool.

On a lightly grazed pasture Adams and Pattison (1985) report NO_3^- leaching losses of 5 kg N/ha for a Wakanui silt loam, a soil closely related to the Templeton silt loam. However, there is no evidence for the leaching of ^{15}N as an explanation for the decline in ^{15}N recovery in the surface soil of the sprayed treatment in this study. No direct measurements were made of NO_3^- leaching, but rainfall and soil moisture data preclude a leaching environment in the soil during the summer of 1988-89, especially in September 1988. Furthermore, in all treatments very little ^{15}N was found in the 10-20 or the 20-60 cm soil depths, and it is highly unlikely that leaching of ^{15}N to below 60 cm depth occurred.

Although the loss was large in terms of quantity of ^{15}N applied it was only about 8 kg N/ha. Given the high ambient concentrations of mineral N in the sprayed treatment after February and slightly moister conditions, it is possible that ^{15}N was lost via localized anaerobic denitrification (Pluth and Nommik, 1981). However, as the heavier isotope of N is discriminated against during biological denitrification (Blackmer and Bremner, 1977), the process may have been more marked than this result suggests.

As already mentioned, most of the ^{15}N retained in the soil was in the 0-20 cm soil depth, which corresponded to the zone of intense rooting by pasture and *P. radiata*. Very little ^{15}N had been moved to below the rooting zone of plants.

10.5 Competition

Caldwell *et al.* (1985) suggested that the examination of some of the mechanisms involved in competition was essential if a better understanding of competition was to be developed. Caldwell *et al.* (1985) used double labelling with ^{32}P and ^{33}P to demonstrate interspecific competition between two species of *Agropyron* and a sagebrush. Although shrub root density and grass root density did not differ, differences in radioisotope content of the grasses and the $^{32}P/^{33}P$ ratio in the sagebrush indicated differential uptake of two P isotopes by the sagebrush. Competitive exploitation was proposed as the mechanism involved in this study. Root competition has been investigated by Bjorkman and Lundeberg (1971) who used ^{15}N and ^{32}P in a regenerating *P. silvestris* forest to examine competition amongst a seed tree, *P. silvestris* seedlings and understorey plants. Levels of atom % excess ^{15}N indicated that competition occurred, although this was not quantified.

In this current study the cumulative recovery of ^{15}N by pasture in the simulated-grazing treatment exemplifies the competitiveness of pasture for available N under trees. However, removing this competition only doubled tree ^{15}N uptake and trees did not recover as much ^{15}N as pasture in the simulated-grazing experiment.

It was shown using $^{15}NO_3^-$ that this form of N remained available longer for plant uptake but again this did not result in greater tree uptake from an application of ^{15}N applied in spring when tree growth was rapid and demand for N should be high. However, pasture appeared to gain some benefit, in terms of N uptake, from the increased availability of $^{15}NO_3^-$.

An early approach to the question of examining competitive interactions for soil moisture and N was made by Watt and Fraser (1933). Their experiment was incomplete but evidence suggested that removing tree competition by trenching resulted in increased understorey biomass due to increased availability of N. Watering did not have any effect.

In the present trenching experiment designed to examine the effects of pine roots on pasture, it was not possible to detect any such effect. This was probably due to the low density of pine roots midway between trees (Houston, 1989, unpub.). There was little evidence of overlapping root systems of neighbouring trees as shown by the very low recoveries of ^{15}N in trees surrounding the central ^{15}N-treated tree, and the lack of tree roots extending beyond 2 m from the trunk.

Houston's (1989, unpub.) study of root distribution undertaken on the trial used in this current study showed there was a highly significant ($P < 0.01$) decline in pine root length (cm/cm^3) between 51 and 153 cm from the tree stem (0.195 and 0.083 cm/cm^3, respectively, in August), and there were no significant differences in pine root length between the rank and sprayed-no-N treatments (0.136 and 0.108 cm/cm^3, respectively, in December).

Pasture root length reported for the rank-no-N treatment by Houston (1989, unpub.) (7.9 to 8.5 cm/cm^3) was low compared with some other estimates for pasture of 330 cm/cm^3 (Barker *et al.*, 1988) and for weeds of 39-52 cm/cm^3 (Nambiar, 1990), but was of a similar magnitude (6 cm/cm^3) to estimates for pasture roots in the surface 20 cm of soil (Evans, 1977).

Similar evidence to this current study has been presented by Smethurst and Nambiar (1989) who showed that higher rooting density of weeds in surface soils compared to *P. radiata* must provide them with some advantage in obtaining nutrients and water.

In this study the ambient mineral N concentrations in the 0-5 and 5-15 cm soil depths were reduced by the presence of pasture. This finding is consistent with other studies where the removal of weed competition also increased soil mineral N concentrations (Nambiar, 1984; Nambiar and Cellier, 1985; Elliot and White, 1987). Similarly foliar N levels increased in the trees when competing vegetation was removed (Nambiar, 1984; Nambiar and Zed, 1980; Nambiar and Cellier, 1985; Smethurst and Nambiar, 1989). Mineral N concentrations, especially NO_3^-, can be reduced under pasture because pasture species, especially grasses, preferentially absorb NO_3^--N (Elliot and White, 1987).

The presence of pasture in this current study, either rank or artificially grazed, did not interfere with the processes of mineralization but did reduce mineral N concentrations. Smethurst and Nambiar (1989) attributed a similar phenomenon, observed in a study of competition between *P. radiata* and weeds during early establishment, to direct competition for N between *P. radiata* seedlings and weeds. In this current study removing pasture competition increased tree N uptake.

In addition, removing pasture competition made more moisture available to trees. Obviously their root system was extensive enough to take advantage of this early in spring as reflected in measurements of growth. It is therefore interesting that this same root system did not allow the tree to benefit more from the increased availability of ^{15}N in this treatment following spraying. Observations of the root systems at the final harvest did not suggest that the trees were exploiting soils beyond 1.9 m radius, although larger roots were definitely more frequent within this radius.

Given that there is little evidence for the presence of many, if any, fine roots at distances from the trees greater than 1.9 m, the rapid drying of soils midway between trees can be attributed solely to pasture. In terms of changes in soil bulk water storage, water was removed from the treatments at distances beyond the influence of trees.

10.6 Future research directions

The outcome of this experiment may suggest that the inclusion of an irrigation treatment in pasture experiments designed to examine competition between trees and pasture may be beneficial. As well as examining competition, such a treatment would be useful in examining the interaction between irrigation and fertilization (Linder *et al.*, 1987). However, inclusion of such a treatment might result in several experimental artifacts such as leaching and lateral movement of nutrients. If such an experiment was to involve the use of ^{15}N then leaching and lateral movement of nutrients, especially N, could create problems, unless special care was taken to control the irrigation treatment.

An alternative may be to study the interaction using species with very distinctive rooting habits or nutrient requirements, or by trenching techniques, as used in this study. Direct effects can be measured without directly watering or removing plants.

This study has demonstrated competition for ^{15}N-labelled fertilizer applied as one application (in a split application program) but did not address in detail competition for water. In competition studies the use of the stable isotopes of hydrogen and oxygen and the dynamics of ^{18}O:^{16}O and D:H ratios in competing vegetation may offer some insight as to the importance of competition for water relative to N. Water uptake and movement within plants has been studied using D:H ratios (White *et al.*, 1985; White, 1988) and ^{18}O:^{16}O ratios have been measured in water-stressed plants (Sternberg, 1988). When these ratios are combined with the use of ^{15}N, it may be possible to develop an experimental design to evaluate both competition for N and water. The source of water uptake by trees and competing vegetation might also be examined (ground water versus rainfall) and concepts parallel to those employed when working with ^{15}N fertilizers could be developed for the study of water uptake and use.

10.7 Conclusions

Pasture growth was most reduced directly under the trees but pasture growth was increased by the addition of N while trees were unable to respond to added N due to the drought conditions. Tree height and root collar diameter growth were reduced during late summer in the pasture treatments compared with the sprayed treatments. Removing pasture competition increased total tree biomass by 56%, an increase that was mainly due to increases in needle, branch and root system biomass.

Soil availability and plant uptake depend on the form of ^{15}N applied and the level of pasture competition. $^{15}NH_4^+$ was rapidly immobilized in the rank and simulated-grazing treatments and pasture uptake of $^{15}NH_4^+$ was significantly lower than $^{15}NO_3^-$ in the first harvest after ^{15}N application.

Availability of $^{15}NH_4^+$ was reduced by pasture competition and immobilization within the first 14 days following application. This resulted in less tree uptake especially in the rank treatment - a phenomenon most likely due to higher root biomass in pasture. Immobilization of $^{15}NO_3^-$ was slower than $^{15}NH_4^+$ but this did not greatly increase tree uptake because pasture was able to compete very effectively for $^{15}NO_3^-$.

The addition of N greatly increased tree and pasture N content. Pasture in the simulated-grazing treatment recovered a greater amount of ^{15}N-labelled fertilizer than pasture in the rank treatment.

P. radiata assimilated the same amount of ^{15}N when added as $^{15}NO_3^-$ or $^{15}NH_4^+$ but the ability of *P. radiata* to utilize ^{15}N-labelled fertilizer applied on one occasion during a program of split fertilizer application was severely limited by the presence of competing pasture.

Overall, the use of the ^{15}N isotope to study the competitive interaction between *P. radiata* and pasture was successful. Competition from either rank pasture or artificially-grazed pasture reduced ^{15}N uptake by *P. radiata*. As well no tree growth response to added N was demonstrated even though some ^{15}N uptake did occur.

Competition for ^{15}N between trees and pasture was localized beneath the tree and did not extend into unoccupied zones between trees. At a distance of 2.5 m from the tree no influence of pine roots on ^{15}N and total N uptake by pasture and pasture production could be demonstrated.

More ^{15}N was retained in litter in the rank treatment than in the sprayed treatment; this process may reduce the loss of ^{15}N and may also act as a source of ^{15}N for future plant uptake.

^{15}N recovery in the combined above and belowground biomass in the simulated-grazing treatment was more than three times as great as in the sprayed treatment and more than twice as great as in the rank treatment. However, pasture competition did not greatly affect ^{15}N recovery in soil. On average, over all treatments, 90% of the ^{15}N-labelled fertilizer applied in spring was recovered.

Soil moisture levels and mineral N concentrations were both lower directly under trees. Removing pasture increased soil moisture and also soil mineral N concentration, tree growth and ^{15}N and total N uptake by *P. radiata*. The pool of plant-available N was increased when pasture competition was removed or by release of N from decaying pasture biomass. Even with the removal of pasture competition soils were drier and mineral N concentrations were lower directly beneath trees than at greater distances from the trees. Therefore, in wide-spaced stands of 4-5-year-old *P. radiata* competition for N and water was very localized.

Pasture is more competitive for N and water because of the nature of its root system which exploits the soil volume more efficiently than tree roots. Tree root systems have a lower root length density than pasture.

The outcome of this study has implications for the practitioner. These are that:

- young *P. radiata* and pasture compete for both N and water,
- competition reduces tree growth during severe droughts,
- removing pasture competition greatly improves tree growth, although weed control need not extend beyond the tree rooting zone,
- different genotypes of *P. radiata* with different rooting habits or tree species adapted to drier conditions may be more suitable for agroforestry systems in low rainfall areas or where drought commonly occurs,
- altering the spatial arrangement of trees and pasture may reduce the effects of competition between trees and pasture.

References

Adams, M.A. and Attiwill, P.M. 1982a. Nitrate reductase activity and growth response of forest species to ammonium and nitrate sources of nitrogen. *Plant and Soil 66:* 373-381.

Adams, M.A. and Attiwill, P.M. 1982b. Nitrogen mineralization and nitrate reduction in forests. *Soil Biology Biochemistry 14:* 197-202.

Adams, M.A., Polglase, P.J., Attiwill, P.M. and Weston, C.J. 1989. *In situ* studies of nitrogen mineralization and uptake in forest soils; some coments on methodology. *Soil Biology Biochemistry 21:* 423-429.

Adams, J.A. and Pattinson, J.M. 1985. Nitrate leaching losses under a legume-based crop rotation in Central Canterbury, New Zealand. *New Zealand Journal of Agricultural Research 28:* 101-107.

Agren, G.I. 1983. Nitrogen productivity of some conifers. *Canadian Journal of Forestry Research 13:* 494-500.

Alexander, I.J. and Fairley, R.I. 1982. Effects of nitrogen fertilisation on populations of fine roots and mycorrhizas in spruce humus. *Plant and Soil 71*: 49-53.

Anderson, G.W. and Batini, F.E. 1979. Clover and crop production under 13- to 15-year old *Pinus radiata. Australian Journal of Experimental Agriculture and Animal Husbandry 19:* 362-368.

Anderson, G.W., Moore, R.W. and Jenkins, P.J. 1988. The integration of pasture, livestock and widely-spaced pine in South Western Australia. *Agroforestry Systems 6:* 195-211.

Andrews, H.P., Snee, R.D. and Sarner, M.H. 1980. Graphical display of means. *The American Statistician 34(4):* 195-199.

Atkinson, D. 1977. Some observations on the root growth of young apple trees and their uptake of nutrients when grown in herbicided strips in grassed orchards. *Plant and Soil 46*: 459-471.

Ballard, R. 1984. Fertilization of plantations. In: Bowen, G.D. and Nambiar, E.K.S. (Eds). *Nutrition of Plantation Forests.* Academic Press, London, pp.327-360.

Balneaves, J.M. 1982. Grass control for radiata pine establishment on droughty sites. *New Zealand Journal of Forestry 27(2):* 259-276.

Balneaves, J.M. 1987. Growth response of radiata pine to area of herbaceous weed control. Proceedings of the 40th Weed and Pest Control Conference. pp.49-51.

Barker, D.J., Zhang, D.M. and MacKay, A.D. 1988. Root distribution in a low fertility hill country sward grazed by sheep. *New Zealand Journal of Experimental Agriculture 16:* 73-76.

Bell, J.P. 1976. Neutron probe practice. *Institute of hydrology, Report No. 19.* Crownmarsh Gifford, Wallingford. 65p.

Benecke, U. 1980. Photosynthesis and transpiration of *Pinus radiata* D. Don under actual conditions in a forest stand. *Oecologia 44*: 192-198.

Beets, J.M. 1977. Measuring soil moisture under pine forest with a Wallingford Probe. Unpublished M.Sc. thesis. University of Waikato, Hamilton, New Zealand.

Beets, P.N. and Pollock, D.S. 1987a. Accumulation and partitioning of dry matter in *Pinus radiata* as related to stand age and thinning. *New Zealand Journal of Forestry Science 17:* 246-271.

Beets, P.N. and Pollock, D.S. 1987b. Uptake and accumulation of nitrogen in *Pinus radiata* stands as related to age and thinning. *New Zealand Journal of Forestry Science 17:* 353-371.

Bevege, D.I. 1984. Wood yield and quality in relation to tree nutrition. In: Bowen, G.D. and Nambiar, E.K.S. (Eds). *Nutrition of forest plantations.* Academic Press, London. pp.293-326.

Binkley, D. and Hart, S. 1989. The components of nitrogen availability assessments in forest soils. *Advances in Soil Science 10:* 57-112.

Birk, E.M. and Vitousek, P.M. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands. *Ecology 67(1):* 69-79.

Bjorkman, B. and Lundeberg, G. 1971. Studies of root competition in a poor pine forest by supply of labelled nitrogen and phosphorus. *Studia Forestalia Suecica No. 91.*

Bjorkman, E., Lundeberg, G. and Nommik, H. 1967. Distribution and balance of ^{15}N-labelled fertilizer nitrogen applied to young pine trees (*Pinus silvestris* L.). *Studia Forestalia Suecica 48.* 23p.

Blackmer, A.M. and Bremner, J.M. 1977. Nitrogen isotope discrimination in denitrification of nitrate in soils. *Soil Biology and Biochemistry 9:* 73-77.

Bowden, R.D., Geballe, G.T. and Bowden, W.D. 1989. Foliar uptake of ^{15}N from simulated cloud water by red spruce (*Picea rubens*) seedlings. *Canadian Journal of Forestry Research 19:* 382-386.

Bowen, G.D. 1984. Tree roots and use of soil nutrients. In: Bowen, G.D. and Nambiar, E.K.S. (Eds). *Nutrition of plantation forests.* Academic Press, London. pp.147-180.

Bremner, J.M. and Mulvaney, C.S. 1982. Nitrogen - total. In: Page, A.L., Miller, R.H. and Keeney, D.R. (Eds). *Methods of soil analysis: Part two - Chemical and microbiological properties.* 2nd edition. Madison, USA. pp.595-624.

Bristow, A.W., Ryden, J.C. and Whitehead, D.C. 1987. The fate at several time intervals of ^{15}N-labelled ammonium nitrate applied to an established grass sward. *Journal of Soil Science 38:* 245-254.

Buresh, R.J., Austin, E.R. and Craswell, E.T. 1982. Analytical methods in ^{15}N research. *Fertilizer Research 3:* 37-62.

Caldwell, M.M., Eissenstat, D.M., Richards, J.H. and Allen, M.F. 1985. Competition for phosphorus: differential uptake from dual-isotope labelled soil interspaces between shrub and grass. *Science 229:* 384-386.

Carlyle, J.C. 1986. Nitrogen cycling in forested ecosystems. *Forestry Abstracts 47(5):* 307-336.

Cellier, K.M. and Stephens, C.G. 1980. Effect of weed control and fertilizer placement on the establishment and early growth of *Pinus radiata* in Southern Australia. *Australian Forestry Research 10:* 361-369.

Chabrol, M., Powlson, D.S. and Hornby, D. 1988. Uptake by maize (*Zea mays* L.) of nitrogen from ^{15}N-labelled dazomet, ^{15}N-labelled fertilizer and from the soil microbial biomass. *Soil Biology and Biochemistry 20:* 517-523.

Clinton, P.W. 1986. Biomass, productivity and nutrient stock of the fine roots of 15-year-old *Pinus radiata* and mixed age *Nothofagus truncata* forests of north-west Nelson. Unpublished M.Sc. thesis. University of Canterbury, Christchurch, New Zealand. 96p.

Cooper, A.B. 1986. Suppression of nitrate formation within an exotic conifer plantation. *Plant and Soil 93:* 383-394.

Cossens, G.G. 1984. Grazed pasture production under *Pinus radiata* in Otago. Proceedings of a technical workshop on Agroforestry. Compiled by Bilbrough, G.W. Dunedin, May 1984. Ministry of Agriculture and Fisheries, Wellington. pp.39-48.

Cromer, R.N., Tompkins, D. and Barr, N.J. 1983. Irrigation of *Pinus radiata* with waste water tree growth in response to treatment. *Australian Forestry Research 13:* 57-65.

Doescher, P.S., Tesch, S.D. and Drewien, W.E. 1989. Water relations and growth of conifer seedlings during three years of cattle grazing on a southwest Oregon plantation. *Northwest Science 63(5):* 232-240.

Dowdell, R.J. and Webster, C.P. 1980. A lysimeter study using nitrogen-15 on the uptake of fertilizer nitrogen by perennial ryegrass swards and losses by leaching. *Journal of Soil Science 31:* 65-75.

During, C. 1984. *Fertilizers and soils in New Zealand farming.* Government Printer, Wellington. 355p.

Dyck, W.J., Mees, C.A. and Hodgkiss, P.D. 1987. Nitrogen availability and comparison to uptake in two New Zealand *Pinus radiata* forests. *New Zealand Journal of Forestry Science 17:* 338-352.

Dyck, W.J., Will, G.M. and Messing, M.G. 1985. The influence of radiata pine forestry on soil. Proceedings of the Soil Dynamics and Land Use Seminar, Blenheim, May 1985.

Edmonds, R.L. and McColl, J.G. 1989. Effects of forest management on soil nitrogen in *Pinus radiata* stands in the Australian Capital Territory. *Forestry Ecology and Management 29*: 199-212.

Elliot, K.J. and White, A.S. 1987. Competitive effects of various grasses and forbs on Ponderosa pine seedlings. *Forestry Science 33*: 356-366.

Ellis, R.C., Webb, D.P., Graley, A.M. and Rout, A.F. 1985. The effect of weed competition and nitrogen nutrition on the growth of seedling *Eucalyptus delegatensis* in a highland area of Tasmania. *Australian Forestry Research 15:* 395-408.

Ennik, G.C. and Baan Hofman, T. 1983. Variation in the root mass of ryegrass types and its ecological consequences. *Netherlands Journal of Agricultural Science 31:* 325-334.

Evans, P.S. 1977. Root distribution and water withdrawal patterns of some crop and pasture species. Proceedings of Soil and Plant Water Symposium. Palmerston North, May, 1976. pp.186-190.

Field, C. and Mooney, H.A. 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givinsh, T.J. *On the economy of plant form and function.* Proceedings of Maria Moors Cabor Symposium. 1983.

Fife, D.N. and Nambiar, E.K.S. 1982. Accumulation and retranslocation of mineral nutrients in developing needles in relation to seasonal growth of young radiata pine trees. *Annals of Botany 50; 817-829.*

Fife, D.N. and Nambiar, E.K.S. 1987. Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. *Annals of Botany 60: 147-156.*

Fisher, F.M. and Gosz, J.R. 1986. Effects of trenching on soil processing and properties in a New Mexico mixed-conifer forest. *Biology and Fertility of Soils 2(1):* 35-42.

Fisher, R.F. and Stone, E.L. 1969. Increased availability of nitrogen and phosphorus in the root zone of conifers. *Proceedings of the American Soil Society 33:* 955-961.

Flewelling, J.W. 1979. Ammonium uptake from dilute solutions by *Pinus radiata* seedlings. *New Zealand Journal of Forestry Science 9:* 10-14.

Floate, M.J.S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In: Clark, F.E. and Russall, T. (Eds) Terrestrial Nitrogen Cycles. *Ecological Bulletin (Stockholm) 33:* 585-601.

Forrest, W.G. and Ovington, J.D. 1970. Organic matter changes in an age series of *Pinus radiata* plantations. *Journal of Applied Ecology 7: 177-186.*

Gadgil, R.L. 1983. Biological nitrogen fixation in forestry: research and practice in Australia and New Zealand. In: Gordon, J.C. and Wheeler, C.T. (Eds). *Biological nitrogen fixation in forest ecosystems: foundations and applications.* Martinus Nijhoff/Dr W. Junk Publishers, The Hague. pp.317-332.

Garwood, E.A. and Williams, T.E. 1967. Growth, water use and nutrient uptake from the subsoil by grass swards. *Journal of Agricultural Science, Cambridge 69:* 125-130.

Greacen, E.L. (Ed.) 1981. Soil water assessment by the neutron method. CSIRO, Melbourne. 140p.

Greacen, E.L., Correll, A.L., Cunningham, R.B., Johns, G.G. and Nicolls, K.D. 1981. Calibration. In: Greacen, E.L. (Ed.) *Soil water assessment by the neutron method.* CSIRO. pp.50-81.

Grottker, T.W. 1984. On the potential of *Pinus radiata* for biomass production for energy in Eyrewell Forest, Canterbury Plains, New Zealand. Unpublished M.For.Sc. thesis, University of Canterbury, New Zealand. 129p.

Hansson, A.C. and Pettersson, R. 1989. Uptake and above and belowground allocation of soil mineral-N and fertilizer-^{15}N in a perennial grass ley (*Festuca pratensis*). *Journal of Applied Ecology 26:* 259-271.

Harris, D. and Paul, E.A. 1989. Automated analysis of ^{15}N and ^{14}C in biological samples. *Communication in Soil Science and Plant Analysis 20(9 & 10):* 935-947.

Hart, R.H., Hughes, R.H., Lewis, C.E. and Monson, W.G. 1970. Effect of nitrogen and shading on yield and quality of grasses grown under young slash pine. *Agronomy Journal 62:* 285-287.

Hauck, R. 1982. Nitrogen - isotope-ratio analysis. In: Page, A.L., Miller, R.H. and Keeney, D.R. (Eds). *Methods of soil analysis: Part two. Chemical and microbiological properties.* 2nd edition. Madison, USA. pp.595-624.

Heal, O.W., Swift, M.J. and Anderson, J.M. 1982. Nitrogen cycling in United Kingdom forests: the relevance of basic ecological research. *Philosophical Transactions of the Royal Society of London. B296:* 427-444.

Hedrick, D.W. and Keniston, R.F. 1966. Grazing and Douglas-fir growth in the Oregon White-Oak type. *Journal of Forestry 64:* 735-738.

✓ Heilman, P.E., Dao Thanh, Cheng, H.H., Webster, S.R. and Harper, S.S. 1982a. Comparison of full spring applications of ^{15}N labelled urea to Douglas-fir. (I) Growth response and nitrogen levels in foliage and soil. *Journal of the American Soil Science Society 46:* 1293-1299.

✓ Heilman, P.E., Dao Thanh, Cheng, H.H., Webster, S.R. and Christensen, L. 1982b. Comparison of fall and spring applications of ^{15}N-labelled urea to Douglas-fir. (II) Fertilizer nitrogen recovery in trees and soil after two years. *Journal of the American Soil Science Society 46:* 1300-1304.

Hoglund, J.H. 1985. Grazing intensity and soil nitrogen accumulation. *Proceedings of New Zealand Grassland Association 46:* 65-69.

Houston, P.A. 1989. Root relationships in radiata pine growing with and without pasture. Unpublished BForSc. dissertation. University of Canterbury, Christchurch, New Zealand. 82p.

Hulm, S.C. and Killham, K. 1990. Response over two growing seasons of a Sitka Spruce stand to ^{15}N-urea fertilizer. *Plant and Soil 124:* 65-72.

Huser, R. 1971. Die umsetzung von ^{15}N-dungern in proben einer Podzol-Braunerde und ihre Ausnutzung durth ein jahrige koniferen. *Plant and Soil 35:* 37-50.

Ismaili, M. and Weaver, R.W. 1986. Competition between siratro and kleingrass for ^{15}N-labelled mineralized nitrogen. *Plant and Soil 96:* 327-335.

Jackson, D.S., Gifford, H.H. and Chittenden, J. 1976. Environmental variables influencing the increment of *Pinus radiata*. (2) Effects of seasonal drought on height and diameter increment. *New Zealand Journal of Forestry Science 5:* 265-286.

Jackson, D.S., Jackson, E.A. and Gifford, H.H. 1983. Soil water in deep pinaki sands: some interactions with thinned and fertilized *Pinus radiata*. *New Zealand Journal of Forestry Science 13(2):* 183-196.

✓ Jackson, L.E., Schimel, J.P. and Firestone, M.K. 1989. Short-term partitioning of nitrate and ammonium between plants and microbes in an annual grassland. *Soil Biology and Biochemistry 21*: 409-415.

Jones, J.M. and Richards, B.N. 1977. Effect of reforestation on turnover of ^{15}N-labelled nitrate and ammonium in relation to changes in soil microflora. *Soil Biology and Biochemistry 9:* 383-392.

Kamphake, L.J., Hannah, S.A. and Cohen, J.M. 1967. Automated analysis for nitrate by hydrazine reduction. *Water Research 1:* 205-216.

Kear, B.S., Gibbs, H.S. and Miller, R.B. 1967. Soils of the downs and plains, Canterbury and North Otago, New Zealand. Soil Bureau Bulletin 14.

√ Keeney, D.R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. *Forestry Science 26:* 159-171.

√ Keeney, D.R. and MacGregor, A.N. 1978. Short-term cycling of ^{15}N-urea in a ryegrass-white clover pasture. *New Zealand Journal of Agricultural Research 21:* 443-448.

Keeney, D.R. and Nelson, D.W. 1982. Nitrogen - inorganic forms. In: Page, A.L., Miller, R.H. and Keeney, D.R. (Eds). *Methods of soil analysis: Part two - Chemical and microbiological properties.* 2nd edition. Madison, USA. pp.643-698.

Knight, P.J. 1973. Influence of nitrogen supply on the growth and branching habit of *Pinus radiata* seedlings. *New Zealand Journal of Forestry 18:* 273-278.

Knowles, R. and Lefebvre, J. 1972. Field, greenhouse and laboratory studies on the transformation and translocation of ^{15}N-labelled urea in a boreal forest black spruce system. In: Proceedings of the symposium on the use of isotopes and radiation in soil-plant relationships including forestry. International Atomic Energy Agency, Vienna, 1972.

Knowles, R.L. and Percival, N.S. 1983. Combinations of *Pinus radiata* and pastoral agriculture on New Zealand hill country: Forestry productivity and economics. In: Hannaway, D.B. (Ed.) Foothills For Food and Forests. *Oregon State University College of Agricultural Sciences, Symposium Series No. 2.*

Ledgard, S.F., Brier, G.J. and Savathchandra, S.U. 1989. Plant uptake and microbial immobilization of ^{15}N labelled ammonium applied to grass-clover pasture. Influence of simulated winter temperature and time of application. *Soil Biology and Biochemistry 21(5):* 667-670.

Ledgard, S.F., Steele, K.W. and Feyten, C. 1988. Influence of time of application on the fate of ^{15}N-labelled urea applied to dairy pasture. *New Zealand Journal of Agricultural Research 31:* 87-91.

Ledig, F.T., Bormann, F.H. and Wenger, K.F. 1970. The distribution of dry matter growth between shoot and roots in loblolly pine. *Botanical Gazette 131*: 349-359.

Lewis, C.E. and Pearson, H.A. 1987. Agroforestry using tame pastures under planted pine. In: Gholz, H.L. (Ed.) *Agroforestry: realities, possibilities and potentials.* pp.195-212.

Lindeberg, T., Bonde, T.A., Bergstrom, L., Pettersson, R., Rosswall, T. and Schnurer, J. 1989. Distribution of ^{15}N in the soil-plant system during a four-year field lysimeter study with barley (*Hordeum distichum* L.) and perennial meadow fescue (*Festuca pratensis* Huds.). *Plant and Soil 119:* 25-37.

Linder, S. and Rook, D.A. 1984. Effects of mineral N on carbon dioxide exchange and partitioning of carbon in trees. In: Bowen, G.D. and Nambiar, E.K.S. (Eds). *Nutrition of forest plantations.* Academic Press, London.

Linder, S., Benson, M.L., Myers, B.J. and Raison, R.J. Canopy dynamics and growth of *P. radiata* 1. Effects of irrigation and fertilization during a drought. *Canadian Journal of Forest Research* 17: 1157-1165.

McColl, R.H.S., White, E. and Gibson, A.R. 1977. Phosphorus and nitrate run-off in hill pasture and forest catchments, Tuita, New Zealand. *New Zealand Journal of Marine and Freshwater Research 11:* 729-744.

McFee, W.W. and Stone, E.L. (Jr) 1968. Ammonium and nitrate as sources for *Pinus radiata* and *Picea glauca. Proceedings of the American Soil Science Society 32:* 879-884.

McGann, R.P. 1983. The climate of Christchurch. *New Zealand Meteorological Service Miscellaneous Publication 167(2).*

McKee, W.H. (Jr) and Wilhite, L.P. 1988. Responses of newly planted loblolly pines to herbicide and nitrogen. *Southern Journal of Applied Forestry 12:* 33-36.

Madgwick, H.A.I., Carey, M.L. and Oliver, G. 1983. The dry matter and nutrient content of aboveground trees in a six-year-old forest farm. Unpublished Production Forestry Division project record. No. 417. 9p.

Madgwick, H.A.I. 1983. Estimation of the oven dry weight of stems, needles, and branches of individual *Pinus radiata* trees. *New Zealand Journal of Forestry Science 13(1):* 108-109.

Madgwick, H.A.I. 1985. Dry matter and nutrient relationships in stands of *Pinus radiata. New Zealand Journal of Forestry Science 15(3):* 324-336.

Madgwick, H.A.I., Jackson, D.S. and Knight, P.J. 1977. Aboveground dry matter, energy, and nutrient contents of trees in an age series of *Pinus radiata* plantations. *New Zealand Journal Forestry Science 7:* 445-468.

Marion, G.M., Miller, P.C. and Black, C.H. 1987. Competition for tracer ^{15}N in tussock tundra ecosystems. *Holaratic Ecology 10*: 230-234.

Marshall, V.G. and McMullan, E.E. 1976. Balance sheet of recovered ^{15}N-labelled urea in a pot trial with *Pseudotsuga menziesii. Canadian Journal of Soil Science 56:* 311-314.

Mead, D.J. 1971. The movement of added nitrogen and phosphorus in a pine forest ecosystem. Unpublished PhD thesis, University of Florida, Florida, USA.

Mead, D.J., Draper, D. and Madgwick, H.A.I. 1984. Dry matter production of a young stand of *Pinus radiata*: some effects of nitrogen fertilizer and thinning. *New Zealand Journal of Forestry Science 14(1):* 97-108.

Mead, D.J. and Gadgil, R.L. 1978. Fertilizer use in established radiata pine stands in New Zealand. *New Zealand Journal of Forestry Science 8(1):* 105-134.

Mead, D.J. and Pritchett, W.L. 1975a. Fertilizer movement in a slash pine ecosystem. (I) Uptake of nitrogen and phosphorus and nitrogen movement in the soil. *Plant and Soil 43:* 451-465.

Mead, D.J. and Pritchett, W.L. 1975b. Fertilizer movement in a slash pine ecosystem. (II) Nitrogen distribution after two growing seasons. *Plant and Soil 43:* 467-478.

Melin, J. 1986. Turnover and distribution of fertilizer nitrogen in three coniferous ecosystems in Central Sweden. Reports in Forest Ecology and Forest Soils, No. 55. Department of Forest Soils, Swedish University of Agricultural Sciences, Uppsala.

Melin, J. and Nommik, H. 1988. Fertilizer nitrogen distribution in a *Pinus sylvestris Pices abies* ecosystem, Central Sweden. *Scandinavian Journal of Forestry Research 3:* 3-15.

Melin, J., Nommik, H., Lohm, U. and Flower-Ellis, J. 1983. Fertilizer nitrogen budget in a Scots pine ecosystem attained by using root isolated plots and ^{15}N tracer technique. *Plant and Soil 74:* 249-263.

Moser, E.B., Saxton, A.M. and Pezeshki, S.R. 1990. Repeated measures analysis of variance: application to tree research. *Canadian Journal of Forestry Research 20:* 524-535.

Nadelhoffer, K.J., Aber, J.D. and Melillo, J.M. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. *Plant and Soil 80*: 321-335.

Nadelhoffer, K.J., Aber, J.D. and Melillo, J.M. 1985. Fine roots, net primary production and soil nitrogen availability: a new hypothesis. *Ecology 66:* 1377-1390.

Nambiar, E.K.S. 1983. Root development and configuration in intensively managed radiata pine plantations. *Plant and Soil 71:* 37-47.

Nambiar, E.K.S. 1984. Significance of first-order lateral roots on the growth of young radiata pine under environmental stress. *Australian Forestry Research 14:* 187-199.

Nambiar, E.K.S. 1990. Interplay between nutrients, water, root growth and productivity in young plantations. *Forest Ecology and Management 30:* 213-232.

Nambiar, E.K.S. and Bowen, G.D. 1986. Uptake, distribution and retranslocation of nitrogen by *Pinus radiata* from ^{15}N labelled fertilizer applied to podzolised sandy soil. *Forestry Ecology and Management 15:* 269-284.

Nambiar, E.K.S. and Cellier, C.M. 1985. Nitrogen fertilizer in establishing *Pinus radiata* plantations on sandy soils: an evaluation of their value. *Australian Forestry 48:* 242-251.

Nambiar, E.K.S. and Fife, D.N. 1987. Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. *Annals of Botany 60:* 147-156.

Nambiar, E.K.S. and Zed, P.G. 1980. Influence of weeds on the water potential, nutrient content and growth of young radiata pine. *Australian Forestry Research 10:* 279-288.

Nelson, D.W. and Sommers, L.E. 1980. Total nitrogen analysis for soil and plant tissues. *Journal of the Association of Official Analytical Chemists 63:* 770-778.

Nicholson, G. 1984. Methods of soil, plant and water analysis. *Forestry Research Institute Bulletin No. 70.* Forest Research Institute, New Zealand Forest Service.

Nommik, H. 1966. The uptake and translocation of fertilizer ^{15}N in young trees of Scotts pine and Norway spruce. *Studia Forestalia Suecica 35.* 16p.

Nommik, H. and Larsson, K. 1989. Assessment of fertilizer nitrogen accumulation in *Pinus sylvestris* trees and retention in soil by ^{15}N recovery technique. *Scandinavian Journal of Forestry Research 4:* 427-442.

O'Connor, K.F. 1986. Roles for forestry in high country land use. *Review 43:* 83-94.

Paavilainen, E. 1973. Studies on the uptake of fertilizer nitrogen by Scots pine using ^{15}N-labelled urea. *Metsantutkimuslaitaksen Jalkaisuja 79.* 47p.

Pang, P.C.K. 1985. Distribution and recovery of ^{15}N after fertilization of Douglas-fir saplings with different nitrogen sources. *Plant and Soil 84(2):* 167-174.

Parfitt, R.L., Joe, E.N. and Cook, F.J. 1985. Water use and pasture growth on Judgeford silt loam. *New Zealand Journal of Agricultural Research 28:* 387-392.

Pastor, J., Aber, J.D., McClaugherty, C.A. and Melillo, J.M. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on blackhawk island, Wisconsin. *Ecology 65(1):* 256-268.

Percival, N.S. and Knowles, R.L. 1988. Relationship between radiata pine and understorey pasture production. Proceedings of the Agroforestry Symposium: Rotorua, 24-27 November, 1986. Piers MacLaren (Ed.) *FRI Bulletin no. 139.* pp.152-164.

Pluth, D.J. and Nommik, H. 1981. Potential denitrification affected by nitrogen source of a previous fertilization of an acid forest soil from central Sweden. *Acta Agriculture Sweden 31:* 235-241.

Preston, C.M., Marshall, V.G., McCullough, K. and Mead D.J. 1990. Fate of ^{15}N-labelled fertilizer applied on snow at two forest sites in British Columbia. *Canadian Journal of Forestry Research: 20* 1583-1592.

Pruden, G., Powlson, D.S. and Jenkinson, D.S. 1985. The measurement of ^{15}N in soil and plant material. *Fertilizer Research 6:* 205-218.

Quinn, B.F. 1982. The influence of grazing animals on nitrogen balances. In: Gander, P.W. (Ed.). *Nitrogen balances in New Zealand ecosystems.* Proceedings of a workshop on nitrogen balances in terrestrial ecosystems in New Zealand. Palmerston North, New Zealand. May 1980. pp.95-102.

Radcliffe, J.E. 1985. Shelterbelt increases dryland pasture growth in Canterbury. *Proceedings of the New Zealand Grassland Association 46:* 51-56.

Raison, R.J., Connell, M.J. and Khanna, P.K. 1987. Methodology for studying fluxes of soil mineral nitrogen in situ. *Soil Biology and Biochemistry 19:* 521-530.

Raison, R.J., Khanna, P.K., Connell, M.J. and Falkiner, R.A. 1990. Effects of water availability and fertilization on nitrogen cycling in a stand of *Pinus radiata. Forestry Ecology and Management 30:* 31-43.

Reeder, J.D. 1984. Errors in concentrating ammonium samples prior to isotope-ratio analysis. *Journal of the Soil Science Society of America 48:* 695-698.

Richards, B.N. 1962. Increased supply of soil nitrogen brought about by *Pinus. Ecology 43(3):* 538-541.

Rook, D.A., Swanson, R.H. and Cranswick, A.M. 1976. Reaction of radiata pine to drought. Soil and Water Symposium, Department of Scientific and Industrial Research, New Zealand. pp.55-68.

Russell, G. and Grace, J. 1979. The effect of windspeed on the growth of grasses. *Journal of Applied Ecology 16:* 507-514.

Sands, R. and Nambiar, E.K.S. 1984. Water relations of *Pinus radiata* in competition with weeds. *Canadian Journal of Forestry Research 14:* 233-237.

Santantonio, D. and Santantonio, E. 1987. Seasonal changes in standing crop of live and dead fine roots during two successive years in a thinned plantation of *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science 17(2/3):* 315-329.

Schepers, J.S., Francis, D.D. and Thompson, M.T. 1989. Simultaneous determination of total carbon, total nitrogen, and ^{15}N on soil and plant material. *Communication in Soil Science and Plant Analysis 20(9 & 10):* 949-959.

Scott, W.R. 1973. Pasture plant nutrition and nutrient cycling. In: Langer, R.H.M. *Pasture and pasture plants.* 428p.

Searle, P.L. 1984. The berthelot or indophenol reaction and its use in the analytical chemistry of nitrogen. *Analyst 109:* 549-565.

Shen, S.M., Pruden, G. and Jenkinson, D.S. 1984. Mineralization and immobilization of nitrogen in fumigated soil and the measurement of microbial biomass nitrogen. *Soil Biology and Biochemistry 16(5):* 437-444.

Smethurst, P.J. and Nambiar E.K.S. 1989. Role of weeds in the management of nitrogen in a young *Pinus radiata* plantation. *New Forests 3:* 203-224.

Smirnoff, N., Todd, P. and Stewart, G.R. 1984. The occurrence of nitrate reductase in the leaves of woody plants. *Annals of Botany 54:* 363-374.

Snowdon, P. and Waring, H.D. 1985. Responses of some genotypes of *Pinus radiata* to clover and fertilization. *Australian Forest Research 15:* 125-134.

Squire, R.O. 1977. Interacting effects of grass competition, fertilizing and cultivation on the early growth of *Pinus radiata* D. Don. *Australian Forestry Research 7:* 247-252.

Steele, K.W. and Percival, N.S. 1984. Nitrogen fertilizer application to pasture under *Pinus radiata. New Zealand Journal of Agricultural Research 27:* 49-55.

Sternberg, L.S.L. 1988. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. In: Rundal, P.W., Ehleringer, J.R. and Nagy, K.A. (Eds). Stable isotopes in ecological research. *Ecological Studies 68.* Springer Verlag, New York. pp.124-141.

Stevenson, G. 1959. Fixation of nitrogen by non-nodulated seed plants. *Annals of Botany 23(92):* 622-635.

Swindel, B.F., Neary, D.G., Comerford, N.B., Rockwood, D.L. and Blakeslee, G.M. 1988. Fertilization and competition control accelerate early southern pine growth on flatwoods. *Southern Journal of Applied Forestry 12(2):* 116-121.

Teare, I.D., Wright, D.L., Stanley, R.L. and Kidd, B.T. 1987. Bahiagrass response to lime and nitrogen under pines. *Agronomy Journal 79(1):* 1-5.

The Editors, 1982. What is agroforestry? Editorial. *Agroforestry Systems 1:* 7-12.

Thomas, R.C. 1987. Retention of ^{15}N labelled urea in a radiata pine ecosystem: effect of split applications. Unpublished PhD thesis. University of Canterbury, Christchurch, New Zealand. 204p.

Van den Driessche, R. 1971. Response of conifer seedlings to nitrate and ammonium sources of nitrogen. *Plant and Soil 34:* 421-439.

Van den Driessche, R. and Dangerfield, J. 1975. Response of Douglas-fir seedlings to nitrate and ammonium nitrogen sources under various environmental conditions. *Plant and Soil 42:* 685-702.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. *The American Naturalist 119(4):* 553-572.

Vitousek, P.M. and Andariese, S.W. 1986. Microbial transformations of labelled nitrogen in a clear-cut pine plantation. *Oecologia 68:* 601-605.

Vitousek, P.M., Gosz, J.R., Grier, C.C., Melillo, J.M. and Reiners, W.A. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological monographs 52(2):* 155-177.

✓ Vitousek, P.M. and Matson, P.A. 1984. Mechanisms of nitrogen retention in forested ecosystems: a field experiment. *Science 225:* 51-52.

✓ Vitousek, P.M., Shearer, G., Kohl, D.H. 1989. Foliar ^{15}N natural abundance in Hawaiian rainforest: patterns and possible mechanisms. *Oecologia 78*: 383-388.

Vose, P.B. 1980. Introduction to nuclear techniques in agronomy and plant biology. Pergamon Press, Oxford. 391p.

Vose, J.M. and Swank, W.T. 1990. Preliminary estimates of foliar absorption of ^{15}N-labelled nitric acid vapour (HNO_3) by mature eastern white pine (*Pinus strobus*). *Canadian Journal of Forestry Research 20:* 857-860.

Walker, T.W., Adams, A.F.R. and Orchiston, H.D. 1956. Fate of labelled nitrate and ammonium nitrogen when applied to grass and clover grown separately and together. *Soil Science 81*: 339-351.

Watson, C.J. 1987. The comparative effects of ammonium nitrate urea or a combined ammonium nitrate urea granular fertilizer on the efficiency of nitrogen recovery by perennial ryegrass. *Fertilizer Research 11(1):* 69-78.

Watt, A.S. and Fraser, G.K. 1933. Tree roots and the field layer. *Journal of Ecology 21:* 404-414.

Webster, C.P. and Dowdell, R.J. 1985. A lysimeter study of the fate of nitrogen applied to perennial ryegrass swards: soil analyses and the final balance sheet. *Journal of Soil Science 36:* 605-611.

Weetman, G.F. and Fournier, R. 1982. Graphical diagnoses of lodgepole pine response to fertilization. *Journal of the American Soil Science Society 16:* 1280-1289.

West, G.G. 1984. Establishment of requirements of *Pinus radiata* cuttings and seedlings compared. *New Zealand Journal of Forestry Science 14(1):* 41-52.

Westermann, D.T. and Crothers, S.E. 1980. Measuring soil nitrogen mineralization under field conditions. *Agronomy Journal 72:* 1009-1012.

White, J.W.C. 1988. Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. In: Rundel, P.W., Ehleringer, J.R. and Nagy, K.A. (Eds). Stable isotopes in ecological research. *Ecological Studies 68.* Springer Verlag, New York. pp.142-162.

White, J.W.C., Cook, E.R., Lawerence, J.R. and Broecker, W.S. 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. *Geochim. Cosmochim. Acta 49:* 237-246.

Whitehead, D.C. and Bristow, A.W. 1990. Transformations of nitrogen following the application of ^{15}N-labelled cattle urine to an established grass sward. *Journal of Applied Ecology 27:* 667-678.

Whitehead, D.C. and Dawson, K.P. 1984. Nitrogen including ^{15}N labelled fertilizer nitrogen in components of a grass sward. *Journal of Applied Ecology 21:* 983-989.

Will, G.M. 1966. Magnesium deficiency: the cause of spring needle-tip chlorosis in young pines on pumice soils. *New Zealand Journal of Forestry 11:* 88-94.

Will, G.M. 1977. The influence of nitrogen supply on the growth form of *Pinus radiata* seedlings. *Forestry Science 23:* 64-68.

Will, G.M. and Stone, E.L. 1967. Pumice soils as a medium for tree growth. Moisture storage capacity. *New Zealand Journal of Forestry 12:* 189-199.

Winer, B.J. 1971. *Statistical principles in experimental design.* Second edition. MacGraw Hill, New York. 907p.

Worsnop, G. and Will, G.M. 1980. Fate of ^{15}N urea fertilizer applied to a recently thinned radiata pine stand on a pumice soil. *New Zealand Journal of Forestry Science 10(2):* 381-394.

Appendices

Appendix 2.1a **Details of monthly additions of nitrogen to plus-N treatments.**

	Month	Monthly addition NH_4^+	Monthly addition NO_3^-	Cumulative total NH_4^+	Cumulative total NO_3^-	Total
AN[1]	April	15	15	15	15	30
Mix[2]	May	11.6	20.9	26.6	35.9	62.5
AN	June	15	15	41.6	50.9	92.5
Mix	July	11.6	20.9	53.2	71.8	125
AN	Aug.	15	15	68.2	86.8	155
Mix	Sept.	11.6	20.9	79.8	107.7	187.5
AN	Oct.	15	15	94.8	122.7	217.5
Mix	Nov.	11.6	20.9	106.4	143.6	250
	Dec.	-				
	Jan.	-				
AN	Feb.	15	15	121.4	158.6	280
Mix	March	11.6	20.9	133	179.5	312.5
AN	April	15	15	148	194.5	342.5

1 Ammonium nitrate fertilizer applied.
2 Mixture of calcium ammonium nitrate and potassium nitrate fertilizers applied.

Appendix 2.1b **Summary of nitrogen additions to plots in the simulated-grazing and plus-N treatments.**

Treatment	Replicate	g/plot	kg N/ha	N removal (kg/ha)	Grazing returns (g/m^2)
Grazing-plus-N	1	502.2	442.8		10.03
	2	491.3	433.3		9.07
	3	521.8	460.2		11.76
	4	505.2	445.5		10.30
	5	508.4	448.3		10.58
	6	507.7	447.7		10.52
	mean		**446.3**	**302.93**	**10.37**
Grazing	1				8.31
	2				8.05
	3				9.76
	4				11.11
	mean		**93.07**	**233.75**	
Rank-plus-N	**mean**	**388.4**	**342.5**	**135.05**	
Rank	**mean**			**72.37**	
Spray-plus-N	**mean**	**388.4**	**342.5**		

Appendix 2.2a **Nutrient concentrations for replicate plots in simulated-grazing treatment at pre-treatment harvests.**

	Replicate	%N	%P	%Ca	%K	%Mg
Grazing-no-N	1	2.08	0.22	0.76	1.65	0.19
	2	2.40	0.22	1.31	1.95	0.24
	1	2.59	0.22	1.10	2.18	0.27
	2	2.86	0.21	1.20	2.55	0.29
	1	2.38	0.21	1.20	2.70	0.27
	2	3.47	0.22	1.35	2.48	0.31
	1	3.51	0.21	1.37	2.90	0.30
	2	3.41	0.21	1.43	2.80	0.32
Grazing-plus-N	1	2.31	0.22	1.15	2.48	0.28
	2	2.65	0.21	1.35	2.30	0.28
	1	2.61	0.20	1.28	2.53	0.32
	2	1.87	0.21	1.32	2.45	0.33
	1	2.65	0.22	1.10	2.55	0.27
	2	3.09	0.21	1.10	2.30	0.25
	1	2.99	0.21	1.10	2.60	0.24
	2	3.41	0.21	1.20	3.15	0.28
	1	1.74	0.20	1.38	2.50	0.32
	2	3.51	0.21	1.02	2.75	0.29
	1	2.31	0.23	0.97	2.80	0.27
	2	2.65	0.22	0.94	3.00	0.26
	1	2.65	0.22	1.08	2.80	0.27
	2	2.92	0.22	1.35	3.08	0.31
	1	2.99	0.22	1.13	3.10	0.29
	2	3.41	0.22	1.12	2.85	0.29

Appendix 2.2b **Summary of pasture nutrient concentrations at pre-treatment harvest for the simulated-grazing treatment.**

	N	P	Ca[1]	K	Mg	n
	mean concentration					
Grazing-no-N	2.83	0.21	1.21	2.40	0.27	8
Grazing-plus-N	2.73	0.21	1.16	2.70	0.28	16

1 : Quantity of Ca returned assuming superphosphate contains 20% Ca (During, 1984) and represents 28 and 30.1% of Ca removed in the simulated-grazing-no-N and plus-N treatments respectively.

There were no significant differences according to ANOVA in nutrient concentrations in a pre-treatment harvest of the simulated-grazing treatment.

Appendix 2.3 Average estimated quantity of nutrients returned in simulated-grazing treatment.

	N	P	Ca[1]	K	Mg	n
			kg/ha			
Grazing-no-N	93.0	7.9	15.43	58.6	11.1	8
Grazing-plus-N	104.0	9.1	18.3	76.0	13.4	16

1. Quantity of Ca returned assuming superphosphate contains 20% Ca (During, 1984) and represents 28 and 30.1% of Ca removed in the simulated-grazing-no-N and plus-N treatments respectively.

For each plot the estimated quantity of nutrients returned to each plot was the average of the products of pre-treatment harvest concentrations and actual weight of dry matter from the two clipped plots within it.

Appendix 2.4a ^{15}N standard sample analysis.

An internal standard was included with each batch of either plant tissue or soil samples analyzed for ^{15}N. Results for these analyses are presented with standard deviations and coefficients of variation as a measure of the long-term reproducibility of ^{15}N analysis. For plant tissue and soil samples the coefficient of variation atom percent ^{15}N were:

			x	s.d.	c.v.
Plant tissue (pine needles)	n=7	%N	1.78	0.068	3.8%
		% ^{15}N	0.3829	0.00047	0.124%
Soil	n=6	%N	0.244	0.005	2.11%
		% ^{15}N	0.3896	0.0005	0.130%

Reproducibility was also tested for a wide range of samples analyzed on two occasions. According to paired T-test these were not significantly different.

Background enrichments used in ^{15}N calculations

	Mean	Coefficent of variation	n
Pine needles	0.3672	0.069	10
Branches, wood and bark	0.3665	0.212	5
Roots	0.3665	-	*
Herbage and roots	0.3665	-	-
Soil	0.3677	0.12	*
Soil extracts	0.3650	-	*

* No sample replication.

Appendix 2.4b Summary of standard sample analyses.

Laboratory used in this study

	Foliage standard	Wood standard	EDTA	Glycine
Mean	1.530	0.0492	101.54	101.24
Standard deviation	0.040	0.0069	2.877	3.27

Mean of 36 laboratories for analysis of standard foliage and wood samples

	Foliage	Wood
Mean	1.471	0.132
Standard deviation	0.111	0.046
Coefficient of variation	7.54%	34.8%

The standard *P. radiata* wood and foliage standard samples used in this study as reference standards were part of the International Union of Forestry Research Organizations inter-laboratory comparison of foliar analyses organized by M.J. Lambert.

Appendix 2.4c Summary of comparison of total nitrogen analysis by sample combustion by Dumas method and acid digestion.

	Mean	Standard deviation	S.E.[1]	n
Dumas combustion	3.54	1.274	0.308	17
Acid digest	3.55	1.315	0.318	17

1 Standard error.

Appendix 2.4d Recovery of KNO_3 crystals.

Mean	Standard deviation	Coefficient of variation
98.33	4.759	4.83

Appendix 2.5 Comparisons of manual and neutron moisture meter methods for estimating water stored in soil profile.

Treatment and tube location	Neutron moisture meter method	Manual method
	mm	
Spray-plus-N at 2.5 m	506.7	510.7
Simulated-grazing-no-N at 2.5 m	415.4	400.8
Simulated-grazing-plus-N at 2.5 m	334.8	357.1
Rank-plus-N at 2.5 m	502.7	472.7
Spray-no-N at 2.5 m	336.9	333.8
Spray-plus-N at 1 m	307.3	283.9
Rank-no-N at 2.5 m	348.1	331.0
Spray-plus-N at 2.5 m	380.0	356.8
$\bar{X}$	391.5	380.8

A paired T test showed that there was no difference in the estimates of the quantity of water stored in the profiles when calculated using either of two methods (P = 0.1266). The mean difference between the two methods was 10.7 mm over the whole profile of approximately 2.7 and 2.8 of the overall mean of the neutron moisture meter and manual methods, respectively.

Appendix 3.1a **Summary of repeated measures analysis of variance for monthly tree height measurements, August 1988-May 1989, adjusted for initial tree size using January 1988 height measurements. Tests of hypothesis of between- and within-subject effects.**

Source	df[1]	F	P[2]	MS[3]
G[4]	2		0.1298	
Pasture v. no pasture	1		0.0002	
Grazing v. rank	1		0.3837	
N[5]	1		0.5250	
G x N	2		0.1258	
Error[a]	17			4337.9
Time	9/9[6]	2.49	0.0946	
Time x G	18/18	1.88	0.0953	
Time x N	9/9	1.53	0.2683	
Time x G x N	18/18	1.01	0.4885	
Covariate	1		0.0001	
Test of separate slopes	5		0.0921	
Error[b]	153			131.5
LSD[7]	20.68			

1 Degrees of freedom.
2 Probability of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to analysis of repeated measures.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.
6 Degrees of freedom from multivariate test. Numerator/denominator.
7 Least significant difference.

Appendix 3.1b Summary of ANCOVA of final tree height adjusted for initial tree size using January 1988 height measurements.

	d[1]	P[2]	MS[3]
G[4]	2	0.0442	
Pasture v. no pasture	1	0.0179	
Grazing v. rank	1	0.4357	
N[5]	1	0.6533	
G x N	2	0.2157	
Covariate	1	0.0001	
Test of separate slopes	5	0.0475	
Error	17		1100.64

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA.
3 Mean square.
4 Level of pasture competition.
5 Monthly additions of N.

Appendix 3.2a **Summary of repeated measures analysis of variance for monthly tree root collar diameter[2] measurements, August 1988-May 1989, adjusted for initial tree size using January 1988 initial root collar diameter measurements. Tests of hypothesis of between- and within-subject effects.**

Source	df[1]	F	P[2]	MS[3]
G[4]	2		0.0041	
Pasture v. no pasture	1		0.0011	
Grazing v. rank	1		0.9073	
N[5]	1		0.4135	
G x N	2		0.8805	
Error	17			9.769.76
Time	9/9[6]	12.36	0.0005	
Time x G	18	5.67	0.0003	
Time x N		1.22	0.3836	
Time x G x N		1.84	0.1026	
Covariate			0.0001	
Test of separate slopes			0.6251	
Error	153			0.0796
LSD[7]	0.508			

1 Degrees of freedom.
2 Probability of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to analysis of repeated measures.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.
6 Degrees of freedom from multivariate test. Numerator/denominator.
7 Least significant difference.

Appendix 3.2b **Summary of ANCOVA of final tree root collar diameter^2 adjusted for initial tree size using January 1988 initial root collar diameter^2 measurements.**

	df[1]	P[2]	MS[3]
G[4]	2	0.0002	
Pasture v. no pasture	1	0.0001	
Grazing v. rank	1	0.9411	
N[5]	1	0.3538	
G x N	2	0.9127	
Covariance	1	0.0001	
Test of separate slopes	5	0.5841	
Error	17		1.6079

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 3.3 **Summary of repeated measures analysis of variance for pasture dry matter production and pasture production, adjusted for pre-treatment harvests, May 1988-May 1989. Tests of hypothesis for between- and within-subject effects.**

		Pasture dry matter production			Pasture production rate		
Source	df[1]	F	P[2]	MS[3]	F	P	MS
N[4]	1		0.0069			0.0245	
Error	21			43186			46.92
Time		15.74	0.0001		16.44	0.0001	
Time x N		1.79	0.1640		1.82	0.1573	
Covariate			0.0926			0.9449	
Test of separate slopes			0.4033			0.3557	
Error	189			42382			51
LSD[5] n = 5.33 (1/4 + 1/8)		321			11.15		

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to repeated measures analysis of variance.
3 Mean square.
4 Monthly addition of N.
5 Least significant difference.

Appendix 3.4a **Summary of ANOVA for total aboveground dry matter produced in the simulated-grazing and rank treatments.**

	df[1]	P[2]	MS[3]
G[4]	1	0.0001	
N[5]	1	0.0001	
G x N	1	0.0004	
Error	36		658702

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 3.4b **Summary of ANOVA for belowground biomass (stubble plus pasture roots) in the top 20 cm of soil.**

		0-10 cm	10-20 cm	0-20 cm
	df[1]		P[2]	
G[3]	1	0.1871	0.8888	0.1915
N[4]	1	0.2955	0.5120	0.3104
G x N	1	0.9386	0.6327	0.9500
			MS[5]	
Error	15	3608469	3258	3712608

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Level of pasture competition.
4 Monthly addition of N.
5 Error mean square.

Appendix 3.5 Covariate analysis.

Treatments were randomly applied to plots of different sized trees necessitating the use of covariance analysis. Two covariates were examined:

(i) (initial diameter of stem 10 cm from ground level)^2
(ii) (initial diameter of stem 10 cm from ground level)^2 x initial height.

Diameters and heights of all trees were measured on 28 January 1988.

It is important to test first for homogeneity of regression slopes between treatments when employing ANCOVA and to ensure that there is a good linear relationship between X and Y (Sokal and Rohlf, 1980, p.499). The covariate also needs to be measured without error.

Linear regression of X and Y was performed:

		Linear regression	
		r^2	P[1]
(Initial root collar diameter)^2	Final tree biomass	0.7106	0.0001
(Initial root collar diameter)^2 x initial height	Final tree biomass	0.7407	0.0001

[1] Probability of regression equation.

In choosing a suitable covariate it was generally assumed that the covariate was not affected in any way by the treatment. Pre-treatment measures of parameters were thus chosen. Table 3.5.1 shows the comparison of two covariates of selected biomass components. In this case initial root collar diameter^2 x initial height was chosen as it gave the best reduction in the error sums of squares term in the ANCOVA for most components and showed the best linear relationship with final tree biomass.

Table 3.5.1 Comparison of three covariates for a range of biomass components at final harvest (adjusted means).

	Grazing		Rank		Spray	
Tree component	Plus-N	No-N	Plus-N	No-N	Plus-N	No-N
			g/tree			
			(initial root collar diameter)^2			
Aboveground tree biomass	28980	26795	27615	25784	45179	42513
Total tree biomass	34312	34297	33760	31087	54764	51197
Current needles	5588	4834	6113	3990	11720	10429
			(initial root collar diameter)^2 x initial height			
Aboveground tree biomass	28287	26859	29109	26410	42763	43439
Total tree biomass	33422	32588	35628	31845	51774	52209
Current needles	5474	4846	6379	4102	11288	10590
			unadjusted data			
Aboveground tree biomass	41010	21318	30867	28100	36978	38595
Total tree biomass	49264	26102	38172	34332	44936	46518
Current needles	7718	3868	6689	4400	10268	9736

Appendix 3.6a **Summary of ANCOVA of oven-dry weights of *P. radiata* biomass components adjusted for initial tree size effects using pre-treatment d^2h.**

	G[1]	Pasture v. no pasture	Grazing v. rank	N[2]	G x N	Covariate	EMS[3]	Test of separate slopes
df[4]	2			1	2	1	17	5
				P[5]				
Foliage								
Current	0.0001	0.0001	0.9381	0.1746	0.6698	0.0001	4154210	0.1099
1-year-old	0.4932	0.2435	0.9191	0.9038	0.9054	0.0001	920414	0.8674
2-year-old	0.4565	0.2736	0.5643	0.5570	0.6096	0.0003	205763	0.0274
Total	0.0003	0.0001	0.9305	0.2897	0.7901	0.0001	7622557	0.3977
Branches								
Current	0.0066	0.0023	0.3640	0.5342	0.4761	0.0034	1224684	0.2993
Older	0.0082	0.0024	0.6243	0.2680	0.8374	0.0001	4290485	0.7405
Stem								
Current	0.0008	0.0002	0.4317	0.4023	0.4919	0.0001	1414516	0.5123
Older	0.6872	0.5842	0.5130	0.1569	0.7120	0.0001	389856	0.6287
Buds	**0.0095**	**0.0027**	**0.7397**	**0.6733**	**0.9377**	0.1655	**55033**	**0.3639**
Bark								
Current	0.0004	0.0001	0.8448	0.1133	0.0461	0.0026	992	0.8223
Older	0.0477	0.0002	0.6026	0.8252	0.0064	0.0001	139971	0.1796
Total aboveground	0.0001	0.0001	0.9507	0.6467	0.8493	0.0001	35142606	0.7288
Roots								
Fine	0.4514	0.4107	0.3369	0.6868	0.5323	0.1377	12930	0.0581
Coarse	0.0010	0.0003	0.5903	0.0775	0.1220	0.0001	551326	0.0046
Stump	0.0211	0.0015	0.2280	0.4694	0.2575	0.0001	336297	0.6622
Total belowground	0.0002	0.0001	0.4210	0.6644	0.4830	0.0001	2704743	0.1201
Total tree	0.0001	0.0001	0.8366	0.6065	0.7985	0.0001	48707273	0.6013

1 Level of pasture competition.
2 Monthly addition of N.
3 Error mean square.
4 Degrees of freedom.
5 Probability of treatment differences according to ANCOVA or, where appropriate probability of differences between specified contrasts.

Appendix 3.6b **Summary of individual treatment regression equations of two-year-old needle biomass and coarse root biomass using pre-treatment d^2h as the independent variable ($n = 4$).**

Two-year-old needle biomass

Treatment	a_o	S.E.[1]	a_i	S.E.	r^2	P^2
Grazing						
Plus-N	-1267.99	644.06	0.044	0.0108	0.8426	0.0539
No-N	32.64	14.88	0.018	0.0003	0.9988	0.0004
Rank						
Plus-N	1257.36	374.28	-0.009	0.008	0.0849	0.3755
No-N	25.29	511.20	0.015	0.0109	0.2308	0.3020
Spray						
Plus-N	31.09	201.11	0.026	0.0042	0.9486	0.1025
No-N	277.65	383.69	0.022	0.0101	0.5572	0.1605
Overall	877.32	810.41	0.055	0.0152	0.4085	0.0026

1 Standard error.
2 Probability of regression equation.

Coarse root biomass

Treatment	a_o	S.E.[1]	a_i	S.E.	r^2	P^2
Grazing						
Plus-N	816.95	961.35	0.041	0.0161	0.6575	0.1216
No-N	171.81	97.76	0.056	0.002	0.9974	0.0230
Rank						
Plus-N	3004.31	1524.62	0.020	0.0258	-0.3367	0.6093
No-N	2693.51	41.80	-0.002	0.0007	0.8102	0.1994
Spray						
Plus-N	1163.24	288.96	0.096	0.006	0.9920	0.0402
No-N	N.D.[3]					
Overall	176.04	176.04	0.018	0.003	0.5350	0.0001

1 Standard error.
2 Probability of regression equation.

Appendix 3.7 Summary of ANOVA of ratios of stem to crown and branches.

	df[1]	Stem[3]:crown[4]	Stem:branches
		P[2]	
G[5]	2	0.0017	0.0703
Pasture v. no pasture	1	0.0100	0.0666
Rank v. grazing	1	0.0660	0.1414
N[6]	1	0.6696	0.6896
G x N	2	0.4969	0.5910
		MS[7]	
Error	18	0.008	0.1502

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Wood plus bark.
4 Foliage plus branches.
5 Level of pasture competition.
6 Monthly addition of N.
7 Mean square.

Appendix 3.8 Total tree root biomass and nitrogen content.

It was only possible to excavate the root systems of 20 of the 26 trees. Total belowground biomass (course roots, stump and fine roots) and N content for the remaining six trees (Table 3.8.1) were estimated using regressions of final root collar on total belowground biomass and N content for the 20 trees sampled. The smallest tree used in developing this regression had a root collar diameter of 8.4 cm.

The regression equations were:

$$\text{total belowground biomass} = -1909.01 + 37.081797 \times \text{final root collar diameter}^2$$
$$(P=0.0001,\ r^2=0.97).$$

A test was made of the regressions of individual treatments and these were found not to be significantly different.

$$\text{N content} = 0.4453 + 0.101496 \times \text{final root collar diameter}^2$$
$$(P=0.0001,\ r^2=0.61).$$

A test was also made of the regression slopes of individual treatments and these were found not to be significantly different.

Table 3.8.1 Estimates of total root biomass and nitrogen content for root systems not sampled.

	Replicate	Total root biomass	N content	Final root collar (cm)
Spray				
No-N	1	6434.4	23.28	15.0
No-N	2	3885.0	16.30	12.5
Plus-N	1	645.6	7.44	8.3
Rank				
No-N	1	645.6	7.44	8.3
Plus-N	1	584.4	7.27	8.2
Grazing				
No-N	1	-437.2	4.47	6.3

Appendix 3.9 Summary of ANOVA for root:shoot ratio at end of experiment.

	df[1]	P[2]	MS[3]
G[4]	2	0.4512	
Pasture v. no pasture	1	0.2178	
Grazing v. rank	1	0.9567	
N[5]	1	0.4231	
G x N	2	0.3687	
Error	12		0.0013

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of specified contrasts.
3 Mean square.
4 Levels of pasture competition.
5 Monthly addition of N.

Appendix 3.10a **Summary of ANOVA for pine fine root biomass less than one millimetre diameter in the top 20 cm of soil.**

	df[2]	P[1] 0-10 cm	MS[3]	10-20 cm	MS
G[4]	2	0.1659		0.7127	
Pasture v. no pasture	1	0.1410		0.4979	
Grazing v. rank	1	0.2213		0.6510	
N[5]	1	0.8316		0.7454	
G x N	2	0.5212		0.1457	
Error	17		11474		943.72

1 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
2 Degrees of freedom.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 3.10b **Summary of ANOVA for the proportion of pine fine root biomass less than one millimetre diameter in the top 10 cm of soil.**

	df[1]	P[2]	MS[3]
G[4]	2	0.0591	
Pasture v. no pasture	1	0.0341	
Grazing v. rank	1	0.2542	
N[5]	1	0.3489	
G x N	2	0.9761	
Error	18		0.01568

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 3.11 **Summary of ANOVA of the ratio of pasture roots and stubble weight to pine fine root weight in the top 20 cm of soil in the 11.341 m^2 plots.**

	df[1]	P[2]	MS[3]
G[4]	1	0.2748	
N[5]	1	0.4183	
G x N	1	0.3215	
Error			2228.98

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 3.12a **Summary of repeated measures analysis of variance for log-transformed needle weight data, October 1988-May 1989, for current and one-year-old needles. Tests of hypothesis of between- and within-subject effects.**

		CNUMC		CNUC		Y1NUC		CNLC		Y1NLC	
Source	df[1]	F	P[2]	F	P	F	P	F	P	F	P
G[3]	2	2	0.4748		0.0009		0.4332		0.0001		0.3217
Pasture v. no pasture	1	1	0.6051		0.0029		0.6453		0.0001		0.2358
Grazing v. rank	1	1	0.2778		0.0065		0.2195		0.0805		0.3458
N[4]	1	2	0.1557		0.1552		0.8160		0.5079		0.7085
G x N	2	17	0.3635		0.2665		0.3968		0.3796		0.9799
EMS[5]	**17**	**136.66**	**0.772**		**0.41**		**0.71**		**0.33**		**0.24**
Time		4.12	0.0001	261.06	0.0001	1.17	0.3724	132.62	0.0001	1.22	0.3808
Time x G		2.94	0.0015	3.03	0.0060	0.54	0.8839	1.21	0.3452	1.61	0.1670
Time x N		1.08	0.0533	1.00	0.4662	0.78	0.6096	2.98	0.0647	0.44	0.8509
Time x G x N			0.4193	0.68	0.7719	0.94	0.5266	0.99	0.4950	1.49	0.2071
EMS			**(df 119) 0.058**		**(df 140) 0.024**		**(df 147) 0.02**		**(df 105) 0.01**		**(df 105) 0.01**

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to analysis of repeated measures.
3 Level of grazing competition.
4 Monthly addition of N.
5 Error mean square.

KEY
- CNUMC Current needles uppermost crown.
- CNUC Current needles upper crown.
- Y1NUC One-year-old needles upper crown.
- CNLC Current needles lower crown.
- Y1NLC One-year-old needles lower crown.

Appendix 3.12b **Monthly individual needle weight treatment means, October 1988-May 1989.**

	Month	Grazing Plus-N	Grazing No-N	Rank Plus-N	Rank No-N	Spray Plus-N	Spray No-N
				mg/needle			
CNUMC	Oct.	11.58	5.45	9.35	5.90	7.90	4.02
	Nov.	13.78	11.0	9.28	10.30	11.80	8.80
	Dec.	21.41	17.60	14.15	17.26	23.15	16.78
	Jan.	26.53	21.80	18.25	19.93	26.95	20.73
	Feb.	31.78	25.35	15.23	23.70	35.75	26.03
	Mar.	32.56	19.05	24.08	24.12	38.80	27.73
	Apr.	31.15	24.30	23.98	25.37	37.98	28.60
	May	34.19	25.90	24.93	26.57	42.05	30.13
CNUC	Oct.	4.85	5.17	4.33	3.83	7.17	4.25
	Nov.	8.09	7.93	6.75	6.43	11.00	5.78
	Dec.	14.74	14.87	10.80	10.55	19.63	14.63
	Jan.	19.20	18.80	13.33	12.98	27.43	19.43
	Feb.	22.48	21.90	16.13	14.83	32.87	26.28
	Mar.	22.83	22.57	16.28	14.68	32.50	26.63
	Apr.	24.75	22.70	15.88	15.38	36.03	24.05
	May	23.58	23.30	16.95	15.95	38.67	28.15
Y1NUC	Oct.	46.58	43.75	36.13	41.05	45.53	43.45
	Nov.	46.38	44.25	37.35	42.08	44.00	42.48
	Dec.	50.71	44.80	37.30	43.63	44.20	41.35
	Jan.	44.35	42.20	30.75	40.88	41.80	43.20
	Feb.	44.85	45.50	33.48	44.08	47.07	43.20
	Mar.	48.03	41.58	34.53	42.20	46.53	42.20
	Apr.	48.73	43.65	35.03	42.33	52.33	38.00
	May	47.49	45.48	35.45	43.60	47.73	45.40
CNLC	Oct.	3.24	3.45	2.73	3.03	3.10	7.07
	Nov.	4.83	4.55	3.90	4.40	6.00	7.27
	Dec.	10.00	10.01	8.53	7.03	13.30	15.10
	Jan.	12.73	12.75	12.30	7.93	20.43	19.97
	Feb.	15.64	14.75	13.20	9.63	26.90	26.13
	Mar.	16.19	15.00	14.63	9.83	26.60	27.23
	Apr.	16.70	15.15	14.30	9.73	28.90	26.80
	May	16.86	15.35	16.10	9.87	30.03	28.17

Appendix 3.12b continued

Y1NLC	Oct.	24.10	26.20	23.47	25.57	26.87	32.87
	Nov.	22.59	22.65	21.17	21.03	23.57	26.60
	Dec.	22.89	22.15	20.03	22.40	23.70	23.27
	Jan.	21.60	20.85	18.90	21.57	21.87	26.93
	Feb.	22.90	22.85	20.50	20.77	24.33	23.30
	Mar.	22.83	24.15	20.63	20.33	22.60	23.17
	Apr.	23.44	25.15	21.67	19.43	25.03	22.17
	May	22.56	23.90	19.00	20.00	23.67	22.80

KEY	CNUMC	Current needles uppermost crown.
	CNUC	Current needles upper crown.
	Y1NUC	One-year-old needles upper crown.
	CNLC	Current needles lower crown.
	Y1NLC	One-year-old needles lower crown.

Appendix 3.13 **Summary of ANOVA and ANCOVA of estimated total number of needles per tree at final harvest using initial d^2h as a covariate.**

	df[1]	P[2]	MS[3]	df	P	MS
G[4]	2	0.9342		2	0.4659	
Pasture v. no pasture	1	0.6739		1	0.2276	
Grazing v. rank	1	0.9753		1	0.8599	
N[5]	1	0.1213		1	0.2663	
G x N	2	0.7439		2	0.9116	
Covariate				1	0.0007	
Error	17		8.6812	16		4.3855
Test of separate slopes	5					0.6946

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square x 10^{10}.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 3.14a Initial biomass and nitrogen content of radiata pine in February 1988.

The trees were felled 18-21 February 1988.

The aboveground biomass of five representative trees was determined in February 1988 at the age of 3.5 years. The trees were harvested as in Section 2.6.1 but all branches and needles were dissected and oven-dried with no subsampling. After oven drying and weighing, samples were bulked for grinding (Section 2.6.7) and analyzed for N (Section 2.9.4). Results are given in Table 3.14.1.

Simple linear regression models were developed to predict weights of tree components and tree N content using diameter breast height (d) and tree height (h).

$$\text{Initial tree N content} = 57.8217 + 0.001618(d^2h)$$

$$r^2 = 0.838,\ P = 0.0187$$

$$\text{Initial aboveground biomass} = 7176 + 0.3008(d^2h)$$

$$r^2 = 0.9457,\ P = 0.0035$$

$$\text{Current needle biomass} = 2454 + 0.0473(d^2h)$$

$$r^2 = 0.78,\ P = 0.0617$$

$$\text{Nitrogen content current needles} = 35.55 + 0.000618(d^2h)$$

$$r^2 = 0.65,\ P = 0.0617$$

Table 3.14.1 Initial aboveground tree biomass and tree N content.

Tree	Initial aboveground tree biomass (g)	Initial aboveground tree N content (g)	d[1] (cm)	h[2] (cm)
1	20611	132.0	9.8	490
2	18065	110.7	8.7	438
3	13083	99.0	6.4	380
4	8551	60.0	4.7	340
5	11540	80.9	6.3	373

1 Diameter at breast height (1.4 m).
2 Tree height.

Appendix 3.14b **Summary regression equations developed from initial biomass harvest of five trees to predict individual biomass component weights.**

Component	a_o	SE[1]	a_i	SE	r^2	P[2]
Older branches	1275.92	714.73	0.06	0.025	0.5276	0.1014
Current branches	932	175.45	0.028	0.0063	0.8250	0.0210
Total bark	354.48	57.83	0.015	0.0020	0.9320	0.005

1 Standard error of parameter.
2 Probability of regression equations.

Appendix 3.14c Data for estimates of branch and bark weight increments.

Treatment	Rep.	Measurements							Regression estimates			Increment estimates		
		cm		g					g			g		
		Height[1]	dbh[1]	Final older bark	Final current bark	Final current branches	Final Y1 branches	Final older branches	Initial current branches	Initial older branches	Initial total bark	Older bark	Y1 branches	Older branches
Grazing-plus-N	1	400	8.0	1867	61.8	2507	4570	8694	1651	2544	752	1115	2919	6150
	2	475	9.3	2483	129.8	2704	4917	4343	2086	4082	992	1491	2831	261
	3	410	7.9	1867	104.7	2202	4228	3903	1651	2543	752	1115	2577	1360
	4	360	6.2	1082	40.4	2506	4141	2351	1321	1375	569	512	2820	976
Grazing-no-N	1	168	1.0	248	26.9	283	264	79	937	17	357	-109	-674	62
	2	215	1.0	277	35.0	344	459	326	939	21	358	-81	-480	304
	3	420	8.6	2469	60.5	2009	5270	1027	1805	3087	837	1633	3465	7174
	4	320	6.1	1188	61.4	2362	3072	3252	1267	1183	539	648	1805	2069
Rank-plus-N	1	192	1.0	364	14.1	378	496	347	938	19	358	6.6	-442	328
	2	380	7.7	1532	118.2	3347	4165	3899	1565	2239	704	828	2600	1660
	3	360	6.1	1312	70.9	2493	4128	4943	1309	1331	562	749	2819	3612
	4	390	8.4	1612	49.7	4897	4962	6429	1705	2734	782	830	3256	3694
Rank-no-N	1	201	1.0	307	18.9	663	671	343	938	20	358	-51	-268	323
	2	400	5.8	1600	77.1	2529	5821	9139	1310	1337	563	1037	4510	7802
	3	395	6.6	1966	78.2	2192	4500	4988	1416	1710	622	1345	3084	3280
	4	365	6.0	1261	95.7	1783	2581	2635	1301	3506	558	702	1279	1329
Spray-plus-N	1	111	1.0	170	40.0	887	351	536	936	11	356	-186	-585	525
	2	255	3.3	1114	88.6	3146	4212	2679	1011	276	398	717	3202	2403
	3	350	6.0	2064	62.0	3577	4485	5300	1286	1252	550	1514	3199	4048
	4	480	9.3	1462	163.3	5252	6388	8288	2098	4125	999	463	4290	4163
Spray-no-N	1	246	1.0	10.5	142.4	5827	5420	2608	939	24	358	677	4481	2584

Table 3.14 continued

2	144	3.6	828	160.8	1909	2576	1931	985	185	384	444	1591	1746
3	425	7.2	3414	222.2	4184	5135	5201	1551	2189	697	2717	3584	3012
4	380	6.7	2925	120.8	2717	4598	9262	1412	1695	619	2306	3186	7567

1 Measured in January 1988.

Appendix 4.1a **Summary of repeated measures analysis of variance of %Ndff and percent ^{15}N recovery in the 0-10 cm soil depth, September 1988-May 1989. Tests of hypothesis for between- and within-subject effects.**

		%Ndff		$\%^{15}N$ recovery	
Source	df[1]	P[2]	MS[3]	P	MS
Treatment	3	0.0081		0.1599	
Pasture v. no pasture	1	0.0396		0.0823	
Grazing v. rank	1	0.1501		0.5272	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.1140		0.8633	
Error	7		0.006		164.96
Time	2	0.2555		0.2633	
Time x treatment	6	0.4415		0.1353	
Error	14		0.011		89.53

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance adjusted by the Huynh-Feldt method where appropriate.
3 Mean square.

Appendix 4.1b **Summary ANOVA for %Ndff and percent ^{15}N recovery in total soil nitrogen in the 0-10 cm soil depth 249 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	%Ndff	^{15}N recovery
		P[2]	
Treatment	3	0.9665	0.9714
Pasture v. no pasture	1	0.7727	0.9379
Grazing v. rank	1	0.7962	0.7824
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.9771	0.6508
		MS[3]	
Error	8	0.0153	182.06

1 Degrees of freedom.
2 Probability from ANOVA of between subject effects in repeated measures analysis of variance.
3 Mean square.

Appendix 4.2a **Summary of repeated measures analysis of variance of %Ndff and percent ^{15}N recovery in 1 M KCl-extractable NH_4^+ and NO_3^- mineral nitrogen in the 0-10 cm soil depth, February 1989 and May 1989. Tests of hypothesis for between- and within-subject effects.**

		%Ndff		$\%^{15}N$ recovery		
		NH_4^+	NO_3^-	NH_4^+	NO_3^-	Total
Source	df[1]			P[2]		
Treatment	3	0.1111	0.7018	0.7216	0.2412	0.3996
Pasture v. no pasture	1	0.4925	0.7027	0.5383	0.1156	0.1297
Grazing v. rank	1	0.1915	0.9025	0.8710	0.9772	0.9487
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.3304	0.3577	0.6210	0.1132	0.3091
EMS[3]	8	1.575	3.176	24.57	50.95	87.39
Time	1	0.3625	0.4368	0.3481	0.5704	0.7952
Time x treatment	3	0.5798	0.1840	0.8137	0.0608	0.0715
EMS	8	0.220	1.868	2.26	25.64	31.17

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Error mean square.

Appendix 4.2b **Summary of repeated measures analysis of variance of the quantity of 1 M KCl-extractable NH_4^+ and NO_3^- mineral nitrogen in the 0-10 cm soil depth, February 1989 and May 1989. Tests of hypothesis for between- and within-subject effects.**

Source	df[1]	NH_4^+		NO_3^-		Total	
		P[2]	MS[3]	P	MS	P	MS
Treatment	2	0.1391		0.1861		0.2261	
Pasture v. no pasture	1	0.8476		0.0839		0.2615	
Grazing v. rank	1	0.0538		0.4017		0.1372	
Error	9		1451.9		1765.8		5540
Time	1	0.7491		0.9994		0.8678	
Time x treatment	2	0.9320		0.0629		0.3163	
Error	9		534.8		531.2		1990

1 Degrees of freedom
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Mean square.

Appendix 4.3a **Summary of ANOVA of the quantity of KCl-extractable mineral nitrogen in the 0-10 cm soil depth, in May 1989, at the end of the experiment.**

		NH_4^+		NO_3^-		Total	
Source	df[1]	P[2]	MS[3]	P	MS	P	MS
Treatment	2	0.3108		0.7561		0.4964	
Pasture v. no pasture	1	0.9935		0.7280		0.8579	
Grazing v. rank	1	0.1424		0.4888		0.2496	
Error	8		1.59		1068		3589

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 4.3b **Summary of ANOVA of the percent ^{15}N in KCl-extractable mineral nitrogen in the 0-10 cm soil depth, in May 1989, at the end of the experiment.**

		NH_4^+		NO_3^-		Total	
Source	df[1]	P[2]	MS[3]	P	MS	P	MS
Treatment	3	0.8827		0.3593		0.6421	
Pasture v. no pasture	1	0.6122		0.9005		0.9084	
Grazing v. rank	1	0.9264		0.8604		0.9166	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.7792		0.1899		0.3231	
Error	8		15.53		58.04		86.29

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 4.4 Summary of repeated measures analysis of variance of the %Ndff and percent ^{15}N recovery in pasture clippings, September 1988-May 1989. Tests of hypothesis for between- and within-subject effects.

		%Ndff		%^{15}N recovery	
Source	df[1]	P[2]	MS[3]	P	MS
Treatment	1	0.2815		0.0422	
Error	4		17.19		3.62
Time	6	0.0001		0.0001	
Time x treatment	6	0.3220		0.0200	
Error	24		4.418		3.323
LSD[4]			4.342		3.765

1 Mean square.
2 Degrees of freedom.
3 Probability of treatment differences according to analysis of repeated measures adjusted by the Huynh-Feldt method.
4 Least significant difference.

Appendix 4.5a **Summary of ANOVA for individual needle nitrogen content of current and one-year-old needles 14 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	CNUMC	CNUC	Y1NUC	CNLC	Y1NLC	Y2NLC
		P[2]					
Treatment	2	0.5217	0.0404	0.4052	0.6866	0.4469	0.1168
Pasture v. no pasture		0.2913	0.0172	0.3953	0.5780	0.7507	0.0908
Grazing v. rank		0.5841	0.1870	0.2478	0.4655	0.2180	0.1248
		MS[3]					
Error	9	75290	511.2	43297	612.2	17388	2189

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.5b **Summary of ANOVA for %Ndff of current and one-year-old needles 14 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	CNUMC	CNUC	Y1NUC	CNLC	Y1NLC	Y2NLC
		P[2]					
Treatment	3	0.3818	0.2879	0.2823	0.3392	0.1862	0.2169
Pasture v. no pasture	1	0.1131	0.0693	0.0792	0.0884	0.0427	0.0506
Grazing v. rank	1	0.7924	0.7773	0.5528	0.7971	0.6717	0.6342
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.9749	0.7092	0.5856	0.5382	0.4523	0.6182
		MS[3]					
Error	8	0.0992	0.375	0.0604	0.5594	0.0365	0.0238

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.5c **Summary of ANOVA for individual needle ^{15}N content of current and one-year-old needles 14 days after ^{15}N-labelled fertilizer application.**

		CNUMC	CNUC	Y1NUC	CNLC	Y1NLC	Y2NLC
Source	df[1]			P[2]			
Treatment	3	0.1492	0.2288	0.2782	0.3034	0.1867	0.1355
Pasture v. no pasture		0.0297	0.0521	0.0782	0.0787	0.0410	0.0292
Grazing v. rank		0.8221	0.7713	0.5266	0.6596	0.9463	0.5863
$^{15}NO_3^-$ v. $^{15}NH_4^+$		0.5784	0.7533	0.6244	0.6308	0.3031	0.4885
				MS[3]			
Error	8	1.303	0.685	8.332	0.2324	0.5840	0.0348

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.6a **Summary of repeated measures analysis of variance of log-transformed nitrogen content of two-year-old needles in the lower crown, September 1988-May 1989. Tests of hypothesis for between- and within-subject effects.**

Source	df[1]	F	P[2]	MS[3]
Treatment	2		0.2002	
Pasture v. no pasture	1		0.3851	
Grazing v. rank	1		0.0937	
Error	8			0.043
Time	2	15.98	0.0016	
Time x treatment	6	6.31	0.0030	
Error	18			0.0011

1 Degrees of freedom.

2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to repeated measures analysis of variance.

3 Mean square.

Appendix 4.6b **Summary of repeated measures analysis of variance of log-transformed %Ndff and ^{15}N content of two-year-old needles in the lower crown, September 1988-May 1989. Tests of hypothesis for between- and within-subject effects.**

		%Ndff		μg ^{15}N/needle	
Source	df[1]	P[2]	MS[3]	P	MS
Treatment	3	0.0702		0.0274	
Pasture v. no pasture	1	0.0250		0.0134	
Grazing v. rank	1	0.3136		0.2090	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.2200		0.1058	
Error	8		0.36		0.34
Time	2	0.0001		0.0033	
Time x treatment	6	0.4058		0.2677	
Error	16		0.04		0.05

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to repeated measures analysis of variance.
3 Mean square.

Appendix 4.7 Seasonal needle nitrogen content for current and one-year-old needles in the plus-nitrogen treatments, October 1988-May 1989; treatment means.

		Grazing	Rank	Spray
		μg N/needle		
CNUMC	14	366.9	256.7	520.0
	50	325.5	209.3	387.7
	113	531.0	356.3	620.3
	154	539.0	239.0	630.3
	249	686.0	550.0	867.3
CNUC	14	90.8	68.0	124.0
	50	168.4	139.7	270.0
	113	338.3	227.3	460.7
	154	330.3	260.0	485.3
	249	441.3	341.7	673.7
Y1NUC	14	997.8	816.0	1032.0
	50	885.5	657.7	905.0
	113	740.5	529.7	690.7
	154	658.8	505.3	702.7
	249	811.5	552.0	719.7
CNLC	14	65.4	52.0	68.3
	50	94.7	75.3	138.0
	113	194.7	183.7	344.3
	154	226.9	191.7	403.0
	249	288.2	269.3	511.1
Y1NLC	14	405.5	529.0	457.0
	50	348.2	343.0	466.5
	113	292.5	236.3	365.5
	154	306.3	242.7	380.5
	249	330.2	253.0	358.0
Y2NLC	14	375.7	319.7	407.7
	154	331.0	271.3	327.0
	249	324.9	285.0	301.7

1 Days since ^{15}N-labelled fertilizer application in September 1988.

KEY
- CNUMC Current needles uppermost crown
- CNUC Current needles upper crown
- Y1NUC One-year-old needles upper crown
- CNLC Current needles lower crown
- Y1LC One-year-old needles lower crown
- Y2NLC Two-year-old needles lower crown

Appendix 4.8a Summary of repeated measures analysis of variance of log-transformed individual needle nitrogen content, September 1988-May 1989, for current and one-year-old needles. Tests of hypothesis of between- and within-subject effects.

		CNUMC		CNUC		Y1NUC		CNLC		Y1NLC	
Source	df[1]	F	P[2]	F	P	F	P	F	P	F	P
Treatment	2		0.0523		0.0119		0.1930		0.0075		0.3281
Pasture v. no pasture	1		0.0575		0.0048		0.3148		0.0023		0.1590
Grazing v. rank	1		0.0513		0.1116		0.0983		0.3553		0.5493
EMS[3]	9		0.49		0.21		0.30		0.17		0.19
Time	4	47.70	0.0001	83.53	0.0001	57.46	0.0001	235.26	0.0001	11.71	0.0094
Time x treatment	8	2.35	0.0875	2.71	0.0585	1.66	0.2064	1.15	0.2503	1.81	0.1864
EMS			(df 36) 0.16		(df 36) 0.02		(df 36) 0.03		(df 36) 0.03		(df 36) 0.01

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to analysis of repeated measures.
3 Error mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown

Appendix 4.8b **Summary of repeated measures analysis of variance of log-transformed %Ndff, September 1988-May 1989, for current and one-year-old needles. Tests of hypothesis of between- and within-subject effects.**

		CNUMC		CNUC		Y1NUC		CNLC		Y1NLC	
Source	df[1]	F	P[2]	F	P	F	P	F	P	F	P
Treatment	3		0.2581		0.0870		0.0463		0.0584		0.0515
Pasture v. no pasture	1		0.0677		0.0351		0.0375		0.0325		0.1068
Grazing v. rank	1		0.5327		0.2381		0.0911		0.2722		0.1381
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1		0.7604		0.3235		0.3007		0.1388		0.1215
EMS[3]	9		1.065		0.68		0.62		0.42		0.33
Time	4	42.87	0.0005	18.43	0.0034	27.53	0.0013	34.38	0.0008	19.26	0.0071
Time x treatment	12	3.22	0.0214	2.691	0.0421	2.71	0.0413	2.15	0.0893	1.58	0.2276
EMS			(df 32) 0.152		(df 32) 0.03		(df 32) .02		(df 32) 0.04		(df 28) 0.02

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to analysis of repeated measures.
3 Error mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown

Appendix 4.8c Summary of repeated measures analysis of variance of log-transformed individual needle ^{15}N content, September 1988-May 1989, for current and one-year-old needles. Tests of hypothesis of between- and within-subject effects.

		CNUMC		CNUC		Y1NUC		CNLC		Y1NLC	
Source	df[1]	F	P[2]	F	P	F	P	F	P	F	P
Treatment	3		0.0850		0.0513		0.0207		0.0363		0.0946
Pasture v. no pasture	1		0.0245		0.0159		0.0242		0.0086		0.0757
Grazing v. rank	1		0.3333		0.1500		0.0402		0.2616		0.2648
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1		0.3354		0.6476		0.2769		0.3418		0.1753
EMS[3]	9		1.99		1.38		0.82		0.89		0.70
Time	4	62.86	0.0002	80.22	0.0001		0.0118		0.0001	4.64	0.0830
Time x treatment	12	1.61	0.1988	3.62	0.0132	10.56	0.0846	133.91	0.0843	1.22	0.3713
EMS			(df 32) 0.191		(df 32) 0.03	2.19	(df 32) .05	13.52	(df 32) 0.04		(df 28) 0.04

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to analysis of repeated measures.
3 Error mean square.

KEY
- CNUMC Current needles uppermost crown
- CNUC Current needles upper crown
- Y1NUC One-year-old needles upper crown
- CNLC Current needles lower crown
- Y1NLC One-year-old needles lower crown

Appendix 4.9a **Summary of ANOVA for individual needle nitrogen content of current and one-year-old needles 249 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	CNUMC	CNUC	Y1NUC	CNLC	Y1NLC	Y2NLC
		P[2]					
Treatment	2	0.1292	0.0349	0.0920	0.0081	0.2081	0.4876
Pasture v. no pasture		0.0604	0.0124	0.7125	0.0026	0.2765	0.9203
Grazing v. rank		0.2914	0.3196	0.0334	0.7557	0.1173	0.2583
		MS[3]					
Error	9	29448	17906	21300	6892	3970	2189

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.9b **Summary of ANOVA for %Ndff of current and one-year-old needles 249 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	CNUMC	CNUC	Y1NUC	CNLC	Y1NLC	Y2NLC
		P[2]					
Treatment	3	0.3753	0.3079	0.2037	0.4095	0.4863	0.2841
Pasture v. no pasture	1	0.1576	0.3386	0.3395	0.3278	0.3607	0.1070
Grazing v. rank	1	0.7885	0.6248	0.4782	0.6375	0.5209	0.8821
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.2851	0.1872	0.1472	0.2684	0.4104	0.2147
		MS[3]					
Error	8	0.0814	0.146	0.0423	0.136	0.042	0.026

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1NLC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.9c **Summary of ANOVA for individual needle ^{15}N content of current and one-year-old needles 249 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	CNUMC	CNUC	Y1NUC	CNLC	Y1NLC	Y2NLC
		p[2]					
Treatment	3	0.2700	0.2400	0.1072	0.1095	0.2775	0.1568
Pasture v. no pasture		0.0762	0.0825	0.4831	0.0266	0.2557	0.1577
Grazing v. rank		0.6161	0.3065	0.0867	0.4016	0.2329	0.7732
$^{15}NO_3^-$ v. $^{15}NH_4^+$		0.4594	0.9167	0.3994	0.9665	0.5076	0.0811
		MS[3]					
Error	8	12.90	9.39	2.76	2.88	0.515	0.243

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

KEY
- CNUMC Current needles uppermost crown
- CNUC Current needles upper crown
- Y1NUC One-year-old needles upper crown
- CNLC Current needles lower crown
- Y1NLC One-year-old needles lower crown
- Y2NLC Two-year-old needles lower crown

Appendix 4.10 **Seasonal course of %Ndff in needles, October 1988-May 1989; treatment means.**

		Grazing		Rank	Spray
		$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$
	Days[1]	%Ndff			
CNUMC	14	0.192	0.201	0.131	0.562
	50	0.632	0.803	0.444	1.368
	113	1.230	0.913	0.571	1.480
	154	0.944	0.753	0.621	1.238
	249	1.140	0.873	0.808	1.155
CNUC	14	0.606	0.413	0.266	1.248
	50	1.236	1.051	0.569	1.808
	113	1.594	1.112	0.696	1.624
	154	1.441	1.112	0.719	1.490
	249	1.484	1.034	0.875	1.230
Y1NUC	14	0.366	0.252	0.128	0.540
	50	0.551	0.426	0.210	0.712
	113	0.751	0.527	0.265	0.715
	154	0.770	0.549	0.315	0.726
	249	0.844	0.574	0.449	0.641
CNLC	14	0.969	0.577	0.414	1.521
	50	1.598	1.073	0.685	1.759
	113	1.700	1.133	0.822	1.590
	154	1.635	1.101	0.892	1.431
	249	1.342	0.983	0.836	1.182
Y1NLC	14	0.330	0.207	0.138	0.286
	50	0.538	0.345	0.232	0.472
	113	0.663	0.449	0.270	0.521
	154	0.665	0.464	0.336	0.556
	249	0.659	0.514	0.401	0.474
Y2NLC	14	0.242	0.177	0.114	0.396
	154	0.458	0.324	0.203	0.497
	249	0.460	0.284	0.264	0.479

1 Days since ^{15}N-labelled fertilizer application in September 1988.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1LC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.11 **Seasonal needle ^{15}N content for current and one-year-old needles, October 1988-May 1989; treatment means.**

	Days[1]	Grazing $^{15}N\text{-}NO_3^-$	Grazing $^{15}NH_4^+$	Rank $^{15}NH_4^+$	Spray $^{15}NH_4^+$
			μg ^{15}N per needle		
CNUMC	14	1.01	0.47	0.25	2.49
	50	2.81	2.03	0.93	5.87
	113	7.17	4.55	2.07	10.16
	154	5.47	4.31	1.54	8.80
	249	8.35	6.07	4.54	10.48
CNUC	14	0.61	0.39	0.18	1.62
	50	1.84	2.14	0.81	5.41
	113	4.79	4.60	1.61	8.07
	154	4.25	4.36	1.92	7.72
	249	5.50	5.77	3.03	8.70
Y1NUC	14	3.84	2.64	1.08	5.98
	50	5.02	4.11	1.41	6.63
	113	6.29	3.76	1.42	4.95
	154	4.66	3.85	1.61	5.24
	249	6.38	5.17	2.53	4.71
CNLC	14	0.60	0.41	0.23	1.00
	50	1.43	1.09	0.53	2.58
	113	3.15	2.59	1.54	5.56
	154	4.34	2.34	1.73	5.88
	249	3.43	3.49	2.26	6.13
Y1NLC	14	1.50	0.81	0.85	1.35
	50	2.03	1.22	0.84	2.28
	113	2.01	1.44	0.67	1.96
	154	1.96	1.59	0.85	2.20
	249	2.20	1.80	1.04	1.75
Y2NLC	14	1.02	0.67	0.40	1.64
	154	1.78	1.05	0.58	1.59
	249	1.71	0.90	0.78	1.39

1 Days since ^{15}N-labelled fertilizer application in September 1988.

KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1NUC One-year-old needles upper crown
CNLC Current needles lower crown
Y1LC One-year-old needles lower crown
Y2NLC Two-year-old needles lower crown

Appendix 4.12 **Summary of ANOVA for needle weight, %Ndff, ^{15}N content and total nitrogen content of senescing needles.**

Source	df[1]	Needle weight (mg)	%Ndff	μg ^{15}N/needle	μg N/needle
			P[2]		
Treatment	3	0.5859	0.1574	0.2177	0.4988
Pasture v. no pasture	1	0.7306	0.0344	0.0866	0.5237
Grazing v. no grazing	1	0.9266	0.8731	0.6762	0.8123
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.2695	0.7201	0.5275	0.1736
			MS[3]		
Error	8	59.7	0.0024	0.002	779.2

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Error mean square.

Appendix 5.1 Summary of repeated measures analysis for quantity of nitrogen removed in the simulated-grazing treatment, May 1988-May 1989.

Source	df[1]	F	P[2]	MS[3]
Treatment	1		0.0001	
Covariate	1		0.0035	
Test of separate slopes			0.0865	
Error				83.36
Time		28.34	0.0001	
Time x treatment		3.02	0.0345	
Error	189			90.05
LSD[4]	11.38			

1 Degrees of freedom.
2 Significance of Wilks Lambda or, where appropriate, probability of treatment differences between subjects according to repeated measures analysis of variance.
3 Mean square.
4 Least significant difference.

Appendix 5.2 Summary of ANOVA of total nitrogen concentrations in *P. radiata* biomass components and pasture roots at the final harvest.

Source		G[1]	Pasture v. no pasture	Grazing v. rank	N[2]	G x N	EMS[3]
	df[4]	2	1	1	1	2	17
				P[5]			
Needles[6]							
CNUMC		0.4273	0.7850	0.2050	0.0945	0.1802	0.0590
CNUC		0.1584	0.9415	0.0586	0.1366	0.2111	0.0360
Y1UC		0.0773	0.4454	0.0341	0.1608	0.2902	0.0252
CNLC		0.0554	0.2572	0.0369	0.8440	0.3046	0.0119
Y1LC		0.0238	0.0523	0.0493	0.8532	0.5203	0.0122
Y2LC		0.1221	0.0903	0.2307	0.8510	0.6017	0.0094
Branches Current		0.8154	0.7477	0.5873	0.2993	0.2699	0.0113
Older		0.1184	0.1010	0.1921	0.0401	0.1465	0.0018
Wood Current		0.0059	0.9514	0.0016	0.0132	0.3916	0.0012
Older		0.1614	0.1318	0.2283	0.0006	0.1245	0.0003
Bark Current		0.0104	0.2877	0.0042	0.0129	0.1408	0.0691
Older		0.0318	0.0820	0.0373	0.3574	0.2706	0.0083
Roots Fine		0.6315	0.9765	0.3450	0.6299	0.7604	0.0071
Coarse		0.1606	0.1298	0.2074	0.4463	0.4109	0.0806
Stump		0.4432	0.3458	0.3772	0.1210	0.6904	0.0021
Buds		0.111	0.0755	0.2477	0.5205	0.0173	0.0597
Pasture roots		0.0214	-	0.0214	0.9551	0.2371	0.0572

1 Level of pasture competition.
2 Monthly addition of N.
3 Error mean square.
4 Degrees of freedom.
5 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
6 KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1UC One-year-old needles upper crown
CNLC Current needles lower crown
Y1LC One-year-old needles lower crown
Y2LC Two-year-old needles lower crown

Appendix 5.3 **Summary of ANOVA of needle nitrogen content at final harvest (μ g N/needle).**

Source	df[1]	Current needles: Uppermost crown	Current needles: Upper crown	Current needles: Lower crown	One-year-old needles: Upper crown	One-year-old needles: Lower crown	Two-year-old needles: Lower crown
		P[2]					
G[3]	2	0.0602	0.0003	0.0003	0.0688	0.0413	0.3895
Pasture v. no pasture	1	0.0339	0.0002	0.0001	0.3591	0.0798	0.3023
Grazing v. rank	1	1.3042	0.0358	0.2177	0.0327	0.0560	0.3287
N[4]	1	0.0435	0.0143	0.1154	0.6085	0.8935	0.7811
G x N	2	0.5670	0.2562	0.7734	0.3389	0.8231	0.7120
		MS[5]					
Error		38128	12774	8312	309028	4551	4770

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Level of pasture competition.
4 Monthly addition of N.
5 Mean square.

Appendix 5.4a **Summary of ANOVA of total nitrogen removed in the simulated-grazing and rank treatments.**

Source	df[1]	P[2]	MS[3]
G[4]	1	0.0001	
N[5]	1	0.0001	
G x N	1	0.7721	
Error	36		90.05

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 5.4b **Summary of ANOVA of total nitrogen content of belowground pasture biomass (stubble plus roots) in the top 20 cm of soil (g/plot).**

Source	df[1]	P[2]	MS[3]
G[4]	1	0.5070	
N[5]	1	0.2388	
G x N	1	1.000	
Error	12		2188.66

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 5.5a Summary of ANCOVA of nitrogen content of *P. radiata* biomass components adjusted for initial tree size effects using pre-treatment d^2h.

Source	G[1]	Pasture v. no pasture	Grazing v. rank	N[2]	G x N	Covariate	EMS[3]	Test of separate slopes
df[4]	2	1	1	1	2	1	17	
				P[5]				
Foliage Current	0.0001	0.0001	0.6481	0.0818	0.7145	0.0001	1419.3	0.0624
1-year-old	0.0832	0.0486	0.2873	0.6441	0.9213	0.0001	141.1	0.3946
2-year-old	0.2444	0.1494	0.3980	0.4226	0.6017	0.0002	22.2	0.0092
Total	0.0001	0.0001	0.4620	0.1067	0.7597	0.0001	2140.6	0.0920
Branches Current	0.0022	0.0006	0.6173	0.3129	0.4141	0.0001	31.2	0.7658
Older	0.0007	0.0002	0.4970	0.6075	0.3244	0.0001	34.1	0.9943
Stem Current	0.0037	0.0078	0.0201	0.0344	0.3433	0.0001	15.4	0.6326
Older	0.0036	0.1203	0.0019	0.0001	0.0635	0.0001	0.74	0.0739
Buds	0.0332	0.0101	0.9700	0.7099	0.6593	0.1308	22.3	0.4471
Bark Current	0.0178	0.0103	0.1869	0.6677	0.1561	0.0058	0.26	0.6118
Older	0.0001	0.0001	0.0706	0.6550	0.1736	0.0001	7.0	0.0270
Total aboveground	0.0001	0.0001	0.3522	0.0915	0.5877	0.0001	3325.8	0.2327
Roots Fine	0.3461	0.5054	0.1969	0.8228	0.3688	0.3315	0.67	0.0310
Coarse	0.0001	0.0001	0.4361	0.0266	0.0551	0.0001	6.3	0.2404
Stump	0.0191	0.0070	0.4292	0.0307	0.9872	0.0001	3.5	0.4280
Total belowground	0.0003	0.0001	0.4324	0.0133	0.0586	0.0001	18.2	0.6186
Total tree	0.0001	0.0001	0.3351	0.0808	0.5370	0.0001	3719.5	0.2640

1 Level of pasture competition.
2 Monthly addition of N.
3 Error mean square.
4 Degrees of freedom.
5 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.

Appendix 5.5b **Summary of individual treatment regressions of two-year-old needle nitrogen content using pre-treatment d^2h as the independent variable (n = 4).**

Treatment	a_o	S.E.[1]	a_i	S.E.	r^2	P[2]
Grazing-plus-N	-13.23	6.02	0.0004	0.0001	0.8758	0.0423
Grazing-no-N	0.50	0.08	0.00017	0.000002	0.9996	0.0001
Rank-plus-N	12.39	3.33	-0.00008	0.00007	0.1002	0.3674
Rank-no-N	-0.29	4.67	0.0001	0.0001	0.3200	0.2606
Spray-plus-N	-0.62	1.02	0.0003	0.00002	0.9910	0.0427
Spray-no-N	0.32	4.20	0.0002	0.0001	0.5387	0.1687
Pooled data	1.64	1.70	0.0001	0.00003	0.5374	0.0001

1 Standard error of parameter.
2 Probability of regression equation.

Appendix 5.6 **Summary of ANOVA for %Ndff in *P. radiata* biomass components, pasture roots and litter.**

Source		Treatment	Pasture v. no pasture	Grazing v. rank	$^{15}NO_3^-$ v. $^{15}NH_4^+$	EMS[1]
	df[2]	3	1	1	1	8
			P[3]			
Needles						
CNUMC		0.3208	0.1175	0.7894	0.2784	0.0788
CNUC		0.2745	0.2429	0.6234	0.1778	0.141
Y1UC		0.1811	0.2597	0.4647	0.1404	0.0408
CNLC		0.3304	0.1836	0.6338	0.2588	0.1315
Y1LC		0.4473	0.2896	0.5148	0.4035	0.0414
Y2LC		0.1862	0.0567	0.8747	0.1882	0.0226
Branches						
Current		0.2529	0.1610	0.6642	0.1775	0.0840
Older		0.2022	0.1488	0.9292	0.0958	0.0496
Wood						
Current		0.2135	0.0906	0.4921	0.2813	0.0594
Older		0.1350	0.7805	0.7238	0.0693	0.0150
Bark						
Current		0.3100	0.0936	0.6353	0.4515	0.0990
Older		0.3229	0.1101	0.6859	0.3563	0.0545
Buds		0.2971	0.1942	0.9782	0.1317	0.0837
Roots						
Fine[5]		0.2887	0.3395	0.1527	0.0971	0.0749
Coarse		0.6558	0.3740	0.6425	0.2930	0.0315
Stump		0.3559	0.0988	0.8098	0.3394	0.0387
Pasture roots		0.6433	-	0.6247	0.6623	0.888
Litter		0.0001	0.0001	0.0005	0.0615	0.0351

1 Error mean square.
2 Degrees of freedom.
3 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
4 KEY
CNUMC Current needles uppermost crown
CNUC Current needles upper crown
Y1UC One-year-old needles upper crown
CNLC Current needles lower crown
Y1LC One-year-old needles lower crown
Y2LC Two-year-old needles lower crown

Appendix 5.7 **Summary of split plot analysis of variance of %Ndff for tree biomass components.**

	df[1]	P[2]	MS[3]
Treatment	3	0.2740	
Component	15	0.0001	
Component x treatment	45	0.1154	
Error	120		0.0168
LSD[4]	0.105		

1 Degrees of freedom.
2 Probability of significant differences according to ANOVA.
3 Mean square.
4 Least significant difference.

Appendix 5.8 Comparison of %Ndff for biomass components of *P. radiata*. (Comparisons significant at $P < 0.05$ level using Scheffes test are indicated by ticks.)

	CNUMC	*CNUC*	*Y1UC*	*CNLC*	*Y1LC*	*Y2LC*	*CBr*	*OBr*	*CW*	*OW*	*CB*	*OB*	*FR*	*CR*	*S*	*Bd*
CNUMC	-		✓		✓	✓				✓			✓			
CNUC		-	✓		✓	✓		✓		✓		✓	✓		✓	
Y1UC	✓	✓	-	✓			✓		✓		✓		✓	✓		✓
CNLC			✓	-	✓	✓		✓		✓		✓	✓			
Y1LC	✓	✓		✓	-		✓		✓		✓		✓	✓	✓	✓
Y2LC	✓	✓		✓		-	✓	✓	✓		✓	✓	✓	✓	✓	✓
CBr			✓		✓	✓	-			✓			✓			
OBr		✓		✓		✓		-		✓			✓			✓
CW			✓		✓	✓			-	✓			✓			
OW	✓	✓		✓			✓	✓	✓	-	✓		✓	✓	✓	✓
CB			✓		✓	✓				✓	-		✓			
OB		✓		✓		✓						-	✓			✓
FR	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	-	✓	✓	✓
CR			✓		✓	✓				✓			✓	-		
S		✓		✓	✓	✓				✓			✓		-	✓
Bd			✓		✓	✓		✓		✓		✓	✓		✓	-

KEY

CNUMC	*Current needles uppermost crown*	*CW*	*Current wood*
CNUC	*Current needles upper crown*	*OW*	*Older wood*
Y1UC	*One-year-old needles upper crown*	*CB*	*Current bark*
CNLC	*Current needles lower crown*	*OB*	*Older bark*
Y1LC	*One-year-old needles lower crown*	*FR*	*Fine roots*
Y2LC	*Two-year-old needles lower crown*	*CR*	*Coarse roots*
CBr	*Current branches*	*S*	*Stump*
OBr	*Older branches*	*Bd*	*Buds*

Appendix 5.9 **Summary of ANOVA of percent ^{15}N recovery in pasture biomass components.**

Source	df[1]	Aboveground	Belowground	Total
			P[2]	
Treatment	3	0.0003	0.5767	0.0173
Grazing v. rank	1	0.0010	0.7117	0.0295
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.0192	0.5119	0.2781
			MS[3]	
Error	5	2.695	3.321	5.236

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 5.10a **Unadjusted ^{15}N-labelled fertilizer recovery in tree biomass components.**

Tree components	Grazing $^{15}NO_3^-$	Grazing $^{15}NH_4^+$	Rank $^{15}NH_4^+$	Spray $^{15}NH_4^+$	S.E.[1]	P[2]
			%			
Foliage						
Current	5.04	4.48	3.56	8.20	0.903	0.0309
1-year-old	1.16	1.34	0.72	1.07	0.273	0.4695
2-year-old	0.16	0.16	0.07	0.13	0.049	0.5443
Total	6.36	5.98	4.35	9.38	1.199	0.0920
Branches						
Current	0.48	0.50	0.46	0.79	0.084	0.0710
Older	0.71	0.76	0.56	0.85	0.165	0.6623
Stem						
Current	0.50	0.57	0.24	0.60	0.111	0.1645
Older	0.16	0.17	0.11	0.08	0.024	0.1050
Bark						
Current	0.037	0.04	0.017	0.043	0.012	0.4584
Older	0.29	0.32	0.14	0.35	0.060	0.1452
Buds	0.14	0.26	0.16	0.37	0.076	0.1997
Total aboveground	8.68	8.59	6.04	12.49	1.61	0.1139
Roots						
Fine[3]	0.12	0.16	0.11	0.11	0.032	0.6477
Coarse	0.33	0.43	0.48	0.53	0.061	0.1889
Stump	0.30	0.33	0.30	0.36	0.058	0.8664
Total belowground	0.75	0.92	0.90	1.01	0.123	0.5479
Total tree	9.43	9.51	6.93	13.49	1.712	0.1325

1 Standard error.
2 Probability of treatment differences according to ANOVA.
3 Roots < 1 mm diameter.

Appendix 5.10b **Single degree of freedom contrasts from ANOVA for percent ^{15}N recovery in tree biomass component.**

	Contrasts		
	Pasture v. no pasture	Rank v. grazing	$^{15}NH_4^+$ v. $^{15}NO_3^-$
Tree components		P^1	
Foliage			
Current	0.0054	0.4888	0.6763
1-year-old	0.9154	0.1435	0.6537
2-year-old	0.7300	0.2345	0.9632
Total	0.0210	0.3656	0.8298
Branches			
Current	0.0162	0.7460	0.8923
Older	0.3625	0.4234	0.8464
Stem			
Current	0.1776	0.0695	0.6833
Older	0.0953	0.1300	0.8476
Bark			
Current	0.3466	0.2148	0.85227
Older	0.1452	0.0693	0.7927
Buds	0.1210	0.3952	0.2971
Total aboveground	0.0304	0.2950	0.9694
Roots			
Fine[2]	0.5453	0.3058	0.3371
Coarse	0.3359	0.5545	0.2809
Stump	0.5186	0.7261	0.7849
Total belowground	0.5382	0.8817	0.3473
Total tree	0.0362	0.3176	0.9743

1 Probability of differences between specified contrasts.

Appendix 5.11 **Single degree of freedom contrasts from ANCOVA for percent ^{15}N recovery in biomass components adjusted for initial tree size differences.**

	Contrasts		
	Pasture v. no pasture	Rank v. grazing	$^{15}NH_4^+$ v. $^{15}NO_3^-$
Tree components		P[1]	
Foliage			
Current	0.0006	0.5966	0.1468
1-year-old	02278	0.1602	0.8372
Total	0.0022	0.4197	0.2452
Branches			
Current	0.0111	0.8971	0.7131
Stem			
Current	0.1300	0.0978	0.9557
Buds	0.0771	0.4883	0.5367
Bark			
Current	0.2495	0.2768	0.9136
Older	0.0799	0.0928	0.8644
Total aboveground	0.0047	0.3366	0.3905
Roots			
Coarse	0.1344	0.4223	0.5454
Stump	0.2028	0.8706	0.8310
Total belowground	0.2648	0.9863	0.6093
Total tree	0.0059	0.3705	0.4476

1 Probability of differences between specified contrasts.

Appendix 5.12a **Summary of ANCOVA of adjusted tree ^{15}N recovery using initial root collar diameter^2 as a covariate.**

Source	df[1]	P[2]	MS[3]
Treatment	3	0.1170	
Pasture v. no pasture	1	0.1453	
Grazing v. rank	1	0.1913	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.2316	
Covariate	1	0.1918	
Error	7		19.58
Test of separate slopes	3	0.5505	

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 5.12b **Summary of ANOVA of adjusted litter ^{15}N recovery.**

Source	df[1]	P[2]	MS[3]
Treatment	1	0.0165	
Pasture v. no pasture	1	0.0052	
Grazing v. rank	1	0.0656	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.9265	
Error	8		1.49

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 5.13 Single degree of freedom contrasts from ANOVA of ^{15}N recovery in the litter component.

Pasture v. no pasture	Grazing v. rank	$^{15}NO_3^-$ v. $^{15}NH_4^+$
	P^1	
0.0069	0.0066	0.6272

1 Probability of differences between specified contrasts.

Appendix 6.1a **Summary of ANOVA of %Ndff in total soil nitrogen in 0-10 and 10-20 cm soil depths at the final sampling.**

Source	df[1]	0-10 cm	10-20 cm
		P[2]	
Treatment	3	0.7930	0.8969
Pasture v. no pasture	1	0.4205	0.9077
Grazing v. rank	1	0.7984	0.4721
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.9773	0.7128
		MS[3]	
Error	8	0.0156	0.0024

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 6.1b **Summary of ANOVA of percent ^{15}N recovery in 0-10 and 10-20 cm soil depths 249 days after ^{15}N-labelled fertilizer application.**

Source	df[1]	0-10 cm	10-20 cm	0-20 cm
			P[2]	
Treatment	3	0.7726	0.9290	0.7750
Pasture v. no pasture	1	0.3352	0.9011	0.3576
Grazing v. rank	1	0.7879	0.5584	0.7000
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.6591	0.6133	0.6003
			MS[3]	
Error	8	191.87	12.32	225.36

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 6.2 **Total nitrogen, atom percent ^{15}N and %Ndff for soils in the 20-60 cm soil depth.**

	Rep.	%N	atom %^{15}N	%Ndff
Grazing-plus-N ($^{15}NO_3^-$)	1	0.161	0.3698	0.039
	2	0.098	0.3720	0.079
Grazing-plus-N ($^{15}NH_4^+$)	1	0.112	0.3695	0.031
	2	0.069	0.3658	NA[1]
Rank-plus-N ($^{15}NH_4^+$)	1	0.058	0.3762	0.146
	3	0.082	0.3769	0.158
Spray-plus-N ($^{15}NH_4^+$)	1	0.075	0.3719	0.072
	2	0.065	0.3606	NA

1 Not calculated as depleted levels were present.

Appendix 6.3 Percent ^{15}N recovery in main ecosystem components and total ^{15}N recovery.

	Rep.	Trees: Aboveground	Trees: Roots	Pasture: Aboveground	Pasture: Roots	Litter	0-10 cm soil	10-20 cm soil	20-60 cm soil	Total[1]	Surrounding tree
					%						
Grazing ($^{15}NO_3^-$)	1	5.32	0.70	42.87	4.33	2.94	43.71	5.98	3.05	105.85	0.06
	2	8.73	0.67	37.33	2.04	1.80	57.13	12.25	3.80	119.95	0.23
	3	11.98	0.88	47.25	2.45	2.00	21.62	7.95	-	94.13	0.33
Grazing ($^{15}NH_4^+$)	1	12.70	1.34	30.10	0.82	1.50	53.73	9.58	1.81	109.77	0.19
	2	7.65	0.84	25.44	7.16	3.01	27.20	9.36	-	80.66	0.05
	3	5.41	0.59	35.60	10.66	3.44	25.99	2.72	-	84.41	0.28
Rank ($^{15}NH_4^+$)	1	5.77	0.96	3.82	3.00	6.88	52.15	9.94	4.44	82.52	0.16
	2	5.71	0.92	11.50	17.89	3.97	28.56	8.85	-	77.40	0
	3	6.63	0.81	7.24	3.21	5.82	35.65	8.12	6.80	67.48	0.70
Sprayed ($^{15}NH_4^+$)	1	10.88	1.03	0.33	-	1.21	54.76	4.89	2.99	73.10	0.04
	2	11.33	0.87	0.32	-	2.17	46.89	6.48	-	68.06	0.55
	3	15.25	1.12	0.06	-	1.45	40.12	13.87	-	71.87	0.30

[1] Includes vegetation and soils to a depth of 20 cm.

Appendix 6.4 Relationship between initial tree size and ^{15}N recovery in several ecosystem components.

	a_o	S.E.[1]	a_i	(S.E.)	n	r^2	P[3]
Tree	9.64	3.94	0.0016	0.0300	12	-0.0997	0.9585
Tree + pasture	17.37	20.16	0.1339	0.1536	12	-0.0222	0.4036
Soil	52.64	15.26	-0.0292	0.1163	12	-0.0931	0.8068
System	71.34	18.85	0.1182	0.1437	12	-0.0303	0.4300

[1] Standard error.
[2] Probability of regression equation.

Appendix 6.5 Summary of ANOVA for total system recovery of ^{15}N.

Source	df[1]	P[2]	MS[3]
Treatment	3	0.0154	
Pasture v. no pasture	1	0.1410	
Grazing v. rank	1	0.1161	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.1325	
$^{15}NO_3^-$ v. others	1	0.0060	
Error	8		120.82

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 6.6 **Summary of ANOVA for ^{15}N recovery in combined above and belowground biomass of trees and pasture 249 days after ^{15}N application.**

Source	df[1]	P[2]	MS[3]
Treatment	3	0.0005	
Pasture v. no pasture	1	0.0049	
Grazing v. rank	1	0.0051	
$^{15}NO_3^-$ v. $^{15}NH_4^+$	1	0.1948	
Error	8		57.32

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 6.7a Estimate of current foliage biomass in surrounding trees.

Regression equations using logarithmic transformation of independent and dependent variables were developed to estimate current foliage biomass from measurements of tree height and root collar diameter.

Data from all treatments were pooled and the validity of the assumption that one equation was applicable across all treatments was found to be correct because slopes of individual treatment equations were not significantly different ($P = 0.6724$).

The equation that gave the best fit was:

Equation 1. *Log current needle biomass = 2.591 + 1.141 (initial root collar diameter)*^{2}

$r^2 = 0.8495$, $P = 0.0001$, EMS = 0.09943.

The procedure described by Madgwick (1983) for converting logarithmic means to arithmetic means with corrections for the resultant skewed distribution was adopted and biomass estimates were therefore multiplied by a factor of 1.051 or exponential x (error mean square)/2.

Appendix 6.7b Estimate of ^{15}N-labelled fertilizer utilized by surrounding trees.

An estimate of fertilizer uptake for trees surrounding the central tree in each plot was made for the four treatments. Samples of current needles in the upper crown from two trees per plot were collected and bulked just after central trees had been harvested. The initial root collar diameter was measured so that foliage biomass could be predicted from regression equation developed in Appendix 6.7a.

The biomass of current needles for each surrounding tree was estimated from Equation 1 (Appendix 6.7a) and ^{15}N uptake was calculated using N content and %Ndff of bulked needle samples from surrounding trees.

$$\textit{Log current needle biomass} = 2.591 + 1.141\ (\textit{initial root collar diameter})^2$$

$r^2 = 0.8495$, $P = 0.0001$, EMS = 0.09943

^{15}N uptake by surrounding trees was estimated from the proportion of ^{15}N fertilizer that occurred in current foliage. This was calculated for each treatment (Table 6.7b.1) and the values were in general higher than those used by Mead (1971) and Thomas (1987), 41 and 47.4% respectively.

Table 6.7b.1 Proportion of ^{15}N fertilizer that occurred in current foliage.

	Simulated-grazing		Rank	Spray
	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NH_4^+$	$^{15}NH_4^+$
		%		
Mean	53.12	47.41	51.06	60.81
Standard dev.	4.22	1.61	6.01	1.67

Table 6.7b.2 Estimates of ^{15}N recovery in surrounding trees for each individual plot in the four treatments.

	$^{15}NO_3^-$			$^{15}NH_4^+$			Rank			Spray		
Replicate	1	2	3	1	2	3	1	2	3	1	2	3
Total	0.06	0.23	0.33	0.19	0.05	0.28	0.16	0	0.70	0.04	0.55	0.30

Appendix 6.7c **Summary of ANOVA of recovery of applied ^{15}N fertilizer in trees surrounding the unconfined treated plots.**

Source	df[1]	P[2]	MS[3]
Treatment	3	0.9010	
Pasture v. no pasture		0.7054	
Grazing v. rank		0.5799	
$^{15}NO_3^-$ v. $^{15}NH_4^+$		0.8695	
Error	8		0.0579

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.

Appendix 6.8 **Proportion of nitrogen derived from ^{15}N-labelled fertilizer in unidentified fungal fruiting bodies.**

	%N	atom %^{15}N	%Ndff
Spray $^{15}NH_4^+$	6.594	0.3684	0.005%
Grazing $^{15}NH_4^+$	6.507	0.3731	0.086%
Background grazing	6.545	0.3681	-

Appendix 7.1 Summary of repeated measures analysis of variance of ambient mineral nitrogen ($NH_4^+ + NO_3^-$) concentrations in the 0-5 and 5-15 cm soil depths, April 1988-May 1989. Trees are considered main plots, distances are subplots. Tests of hypothesis for between- and within-subject effects.

		0-5 cm			5-15 cm		
Source	df[1]	F	P[2]	MS[3]	F	P	MS
G[4]	2	26.28	*		2.28	ns	
Pasture v. no pasture	1	20.71	**		4.55	ns	
Grazing v. rank	1	5.57	ns		0.02	ns	
N[5]	1	34.35	**		12.59	*	
G x N	2	8.87	*		1.37	ns	
Error	6			10430.6			660.7
D[6]	1	2.04	0.2029		4.26	0.0845	
D x G	2	2.75	0.1417		2.13	0.7647	
D x N	1	0	0.9599		0.10	0.2202	
D x G x N	2	0.58	0.5887		0.22	0.8068	
Error	6			4389.2			254.0
Time	13	24.97	***		12.27	***	
Time x N	26	3.87	***		1.58	*	
Time x G	13	5.74	***		3.02	***	
Time x G x N	26	1.72	*		1.13	ns	
Time x D	13	0.60	ns		1.36	ns	
Time x D x G	26	1.69	*		1.46	ns	
Time x D x N	13	0.96	ns		2.36	ns	
Time x D x N x G	26	1.20	ns		0.65	ns	
Error	156			2857.1			139.54

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.
6 Distance from stem, 1 or 2.5 m.
ns Non significant.
* P<0.05
** P<0.01
*** P<0.005

Appendix 7.2a **Summary of repeated measures analysis of variance of the change in NH_4^+ and NO_3^- concentrations in the 0-5 and 5-15 cm soil depths, April 1988-April 1989. Tests of hypothesis of between- and within-subject effects.**

		0-5 cm						5-15 cm					
		NH_4^+			NO_3^-			NH_4^+			NO_3^-		
Source	df[1]	F	P[2]	MS[3]	F	P	MS	F	P	MS	F	P	MS
G[4]	2	1.13	ns		1.55	ns		2.64	ns		0.75	ns	
Pasture v. no pasture	1	1.21	ns		2.36	ns		2.15	ns		1.48	ns	
Grazing v. rank	1	1.05	ns		0.73	ns		3.11	ns		0.02	ns	
N[5]	1	2.07	ns		6.46	*		0.43	ns		0.17	ns	
G x N	2	0.23	ns		1.43	ns		0.42	ns		0.86	ns	
Error	6			1522.3			1906.1			21.2			44.1
D[6]	1	1.17	0.3213		8.19	0.0287		0.42	0.5429		0	0.9464	
D x G	2	13.78	0.0057		6.68	0.0297		5.83	0.0392		0.52	0.6203	
D x N	1	0.29	0.0067		2.22	0.1867		2.26	0.6815		0.44	0.5315	
D x G x N	2	10.55	0.0108		10.35	0.0113		1.78	0.2465		0.71	0.5273	
Error	6						384.7			12.21			376.1
Time	12	2.74	***		4.59	***		3.43	***		4.65	***	
Time x G	24	0.71	ns		0.83	ns		1.39	ns		1.84	*	
Time x N	12	2.12	*		2.37	***		0.44	ns		1.03	ns	
Time x G x N	24	0.61	ns		1.00	ns		0.87	ns		0.96	ns	
Time x D	12	1.96	*		0.54	ns		0.80	ns		1.17	ns	
Time x G x D	24	2.40	***		1.01	ns		0.71	ns		0.87	ns	
Time x D x N	12	0.92	ns		0.99	ns		0.92	ns		1.08	ns	
Time x G x N x D	24	0.92	ns		1.05	ns		0.87	ns		0.70	ns	
Error	144			1248.6			1647.5			29.91			145.9

1 Degrees of freedom
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.
6 Distance from stem, 1 or 2.5 m.

ns non significant, $P < 0.05$, $P < 0.01$, $P < 0.005$

Appendix 7.2b **Summary of means from repeated measures analysis of variance of change in NH_4^+-N during incubations in the 5-15 cm soil depth, April 1988-April 1989.**

	Simulated-grazing		Rank		Spray	
	1 m	1 - 2.5 m	1 m	1 - 2.5 m	1 m	1 - 2.5 m
April 1988	-1.35	-1.23	-0.03	6.43	-0.98	-1.40
May	1.68	0	2.68	-1.83	2.30	2.20
June	5.98	2.25	0.95	-4.05	-3.93	-0.23
July	-0.15	-1.23	-1.40	-2.28	-3.33	-1.38
Aug.	-0.35	1.83	0.28	0.55	1.83	-2.45
Sep.	-0.75	3.03	0	0.63	0.93	4.03
Oct.	-1.78	1.28	-3.58	-12.95	-0.35	-2.75
Nov.	3.38	6.35	3.45	2.38	0.90	-0.50
Dec.	1.23	2.28	6.63	4.75	0.93	0.55
Jan.	-0.28	15.15	2.03	1.85	0.63	4.48
Feb.	-1.40	-4.58	-2.23	-3.08	-1.90	1.73
Mar.	-0.73	-0.05	3.78	-0.65	1.20	0.83
April 1989	-0.98	2.25	-1.25	-0.35	-3.63	-3.63

Appendix 7.3 Summary of repeated measures analysis of variance of net nitrogen mineralized in the 0-5 and 5-15 cm soil depths, April 1988-April 1989. Tests of hypothesis of between- and within-subject effects.

		0-5 cm		5-15 cm	
Source	df[1]	P[2]	MS[3]	P	MS
G[4]	2	0.1991		0.4604	
Pasture v. no pasture	1	0.1796		0.6001	
Grazing v. rank	1	0.2101		0.2170	
N[5]	1	0.0391		0.7405	
G x N	2	0.1000		0.6662	
Error	6		4397.19		1713.75
Time	12	0.0052		0.0006	
Time x G	24	0.1933		0.3963	
Time x N	12	0.0598		0.7084	
Time x G x N	24	0.3162		0.8756	
Error	144		5971.39		1458.51

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 7.4 Summary of ANOVA of cumulative net nitrogen mineralized and the increment in mineral nitrogen in both 0-5 and 5-15 cm soil depths, April 1988-April 1989.

		N mineralized			Increment in mineral N	
		0-5 cm	5-15 cm	Total	0-5 cm	5-15 cm
Source	df[1]			P[2]		
G[3]	2	0.1992	0.4598	0.1444	0.2442	0.3351
Pasture v. no pasture	1	0.1797	0.5989	0.0698	0.3431	0.2749
Grazing v. rank	1	0.2102	0.2715	0.4733	0.1620	0.3162
N[4]	1	0.0391	0.7397	0.0292	0.0091	0.0142
G x N	2	0.0999	0.6657	0.0502	0.5595	0.2885
				MS[5]		
Error	6	57164	22259	40966	7261	2108

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Level of pasture competition.
4 Monthly addition of N.
5 Mean square.

Appendix 7.5 Summary of ANOVA for proportion of NO_3^--N in net nitrogen mineralized in the incubated cores in the combined 0-15 cm soil depth.

Source	df[1]	P[2]	MS[3]
G[4]	2	0.1980	
Pasture v. no pasture	1	0.1620	
Grazing v. rank	1	0.2338	
N[5]	1	0.5393	
G x N	2	0.7508	
Error	6		1785.4

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 7.6 Summary of ANOVA of cumulative nitrogen mineralized, change in mineral nitrogen storage in soil in the 0-15 cm soil depth, and nitrogen uptake into aboveground vegetation (trees plus pasture) and uptake (Dyck *et al.*, 1987).

		P[1]			
Source	df[2]	N mineralized	Change in N stored	N uptake aboveground	Apparent N uptake
G[3]	2	0.1444	0.2343	0.1860	0.2653
Pasture v. no pasture	1	0.0698	0.2839	0.1274	0.2162
Grazing v. rank	1	0.4733	0.1763	0.2837	0.2773
N[4]	1	0.0292	0.0076	0.4845	0.0023
G x N	2	0.0502	0.6317	0.3084	0.0207
		MS[5]			
Error	6	40966	14739	13792	23516

1 Probability of treatment differences according to ANOVA or, where appropriate, probability of differences between specified contrasts.
2 Degrees of freedom.
3 Level of pasture competition.
4 Monthly addition of N.
5 Mean square.

Appendix 8.1 Summary of repeated measures analysis of variance of θ in 0-10 cm horizon, April 1988-May 1989; distances are subplots. Tests of hypothesis for between- and within-subject effects.

Source	df[1]	F	P[2]	MS[3]
G[4]	2	4.119	NS[7]	
N[5]	2	0.75	NS	
G x N	2	0.04	NS	
Error	5			0.0112
D[6]	1	131.26	0.0001	
D x G	2	5.48	0.0550	
D x N	1	0.02	0.8808	
D x G x N	1	0.25	0.6404	
Error	5			0.0005
Time	13	38.67	***[8]	
Time x G	26	1.98	***	
Time x N	13	0.92	NS	
Time x G x N	26	0.91	NS	
Time x D	12	2.20	**	
Time x D x G	26	0.41	NS	
Time x D x N	13	0.41	NS	
Time x D x G x N	13	0.43	NS	
Error	130			0.00138

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Mean square.
4 Level of pasture competition.
5 Monthly addition of N.
6 Distance from stem, 1 or 2.5 m.
7 Non significant.
8 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

Appendix 8.2 Summary of ANOVA for soil moisture deficit on 15 September 1988 in the 10-100 cm soil depth.

	df[1]	F	P[2]	MS[3]
G[4]	1	0.774	0.4968	
Error	6			1096.8
D[5]	1	22.34	0.0052	
G x D	1	1.67	0.2531	
Error	14			340.8

1 Degrees of freedom.
2 Probability of treatment differences.
3 Mean square.
4 Level of pasture competition.
5 Distance.

Appendix 8.3 Summary repeated measures analysis of variance of soil moisture deficit in 10-100 cm horizon, 15 September 1989-29 April 1989; distances are subplots. Tests of hypothesis for between- and within-subject effects.

Source	df[1]	F	P[2]	MS[3]
G[4]	1	8.35	*[5]	
Error	6			14643.1
D[6]	1	15.40	0.0111	
G x D	1	10.31	0.0237	
Error	5			1176.5
Time	31	59.43	***	
Time x G	31	1.95	***	
Time x D	31	9.29	***	
Time x G x D	31	2.63	***	
Error	311			69.63

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance.
3 Mean square.
4 Level of pasture competition.
5 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

Appendix 8.4 Summary of ANOVA for change in soil moisture deficit, 15 September 1988-29 April 1989 in the 10-100 cm soil depth.

	df[1]	F	P[2]	MS[3]
G[4]	1	0.63	0.6480	
Error	6			657.31
D[5]	1	18.99	0.0073	
G x D	1	1.43	0.2853	
Error	14			340.4

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.
4 Level of pasture competition.
5 Distance.

Appendix 8.5 Summary of minimum and peak soil moisture contents for 10-50 and 50-100 cm soil depths at both distances sampled.

				Peak soil moisture content				Minimum soil moisture content			
		Distance		10-50		50-100		10-50		50-100	
Treatment	**Establishment date**	1.0 m	2.5 m	**Date**	mm	**Date**	mm	**Date**	mm	**Date**	mm
Grazing-plus-N	26/5			28/7	89.7	22/9	118.9	23/3	57.2	23/3	85.6
	26/5			21/7	145.1	4/8	83.2	16/3	63.6	12/3	86.5
	1/9			1/9	125.1	15/9	96.1	7/1	52.9	30/3	50.5
Grazing-no-N	31/5			21/7	89.4	18/8	111.4	16/3	59.5	23/3	77.8
	1/9			1/9	122.6	15/9	73.1	26/1	52.4	23/3	77.2
Rank-plus-N	26/5			21/7	110.7	28/7	84.4	16/3	60.4	8/4	56.7
	1/9			1/9	135.0	15/9	127.2	7/1	56.8	12/3	57.2
Rank-no-N	31/5			25/8	146.5	15/9	129.1	16/3	60.7	23/3	83.0
	23/6			25/8	143.3	13/10	106.6	7/1	59.1	30/3	81.5
Spray-plus-N	31/5			25/8	123.3	15/9	132.5	16/3	74.1	23/3	98.7
	15/9			15/9	143.5	10/11	106.9	16/3	74.8	8/4	104.1
	15/9			15/9	95.4	15/9	131.7	16/3	70.1	8/4	95.4
	21/7			25/8	144.9	15/9	105.4	16/3	70.9	29/4	90.2
Spray-no-N	31/5			25/8	94.0	29/9	123.7	16/3	76.4	16/3	95.0
	15/9			15/9	132.6	15/9	123.7	16/3	78.2	8/4	103.5

Field capacity = 300 mm for 10-100 cm soil depth.

Appendix 9.1 **Summary of repeated measures analysis of variance for dry matter production, nitrogen concentration and nitrogen removed in trenching experiment, September 1988-September 1989; trenching treatments are considered subplots. Tests of hypothesis for between- and within-subject effects.**

	Dry matter				N concentration				N removed			
Source	df[1]	F	P[2]	MS[3]	df	F	P	MS	df	F	P	MS
N[4]	1	0.386	NS[5]		1	0.179	NS		1	0.877	NS	
Error	4			1519.6	4			0.212	4			1.082
T[6]	1	3.30	0.1435		1	0.07	0.8065		1	2.538	0.1892	
T x N	1	0.57	0.4939		1	0.72	0.4598		1	0.09	0.7804	
Error	4			1341.1	3			0.504	3			0.886
Time	7	86.84	***[7]		7	32.23	***		7	80.71	***	
Time x N	7	0.32	NS		7	2.329	NS		7	0.201	NS	
Time x T	7	1.08	NS		7	0.823	NS		7	0.475	NS	
Time x T x N	7	1.56	NS		7	1.197	NS		7	0.623	NS	
Error	56			1584.7	49			0.117	49			2.24

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance adjusted by the Huynh-Feldt method.
3 Mean square.
4 Monthly addition of N.
5 Non significant.
6 Trenching treatment.
7 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

Appendix 9.2 Summary of ANOVA of total dry matter and nitrogen removal from trenching experiment.

	Dry weight (m^2)				Nitrogen (m^2)		
Source	df[1]	F	P[2]	MS[3]	F	P	MS
N[4]	1	0.24	NS[5]		2.23	NS	
Error	4			14310.5			19.69
T[6]	1	2.98	0.1595		4.10	0.1129	
N x T	2	0.46	0.5361		0.39	0.5662	
Error	4			11043.7			18.08

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.
4 Monthly addition of N.
5 Non significant.
6 Trenching treatment.

Appendix 9.3 Summary of analysis of repeated measures for %Ndff and percent ^{15}N recovery in pasture for trenching experiment, September 1988-September 1989. Tests of hypothesis for between- and within-subject effects.

		%Ndff			%^{15}N recovery		
Source	df[1]	F	P[2]	MS[3]	F	P	MS
T[4]	1	0.60	0.4813		0.11	0.7536	
Error	4			22.12			16.798
Time	7	11.19	0.0048		17.57	0.0032	
Time x T	7	0.49	0.6299		1.53	0.2787	
Error	28			4.226			4.872

1 Degrees of freedom.
2 Probability of treatment differences according to repeated measures analysis of variance adjusted by the Huynh-Feldt method.
3 Mean square.
4 Trenching treatment.

Appendix 9.4 Individual plot data for ^{15}N recovery by components for trenching experiment.

		Trenched	Untrenched
Herbage	1	47.11	35.53
	2	20.19	21.06
	3	23.88	25.04
Soil	1	75.6	52.6
	2	16.4	21.1
	3	25.6	27.8
Total	1	122.7	88.2
	2	36.5	42.2
	3	49.5	52.8

Appendix 9.5 Summary of ANOVA of gravimetric soil moisture content in trenched and untrenched plots at the end of the experiment.

		Soil depth (cm)		
		0-10	10-20	20-50
	Df[1]		P[2]	
Trench	1	0.7863	0.0030	0.7380
			MS[3]	
Error	15	0.409	0.279	3.761

1 Degrees of freedom.
2 Probability of treatment differences according to ANOVA.
3 Mean square.

Appendix 10.1 **Summary of ANCOVA of ratio aboveground biomass: aboveground nitrogen content of *P. radiata* using initial root collar diameter^2 as a covariate.**

	df[1]	P[2]	EMS[3]
G[4]	2	0.0001	
Pasture v. no pasture	1	0.0001	
Grazing v. rank	1	0.0033	
N[5]	1	0.0001	
G x N	2	0.0149	
Covariate	1	0.0072	
Error	17		67.29
Test of separate slopes		0.4638	

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Error mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 10.2 Summary of ANOVA of ratio of current wood weight:weight of total needle nitrogen content of *P. radiata*.

	df[1]	P[2]	EMS[3]
G[4]	2	0.3255	
Pasture v. no pasture	1	0.1682	
Grazing v. rank	1	0.5732	
N[5]	1	0.0728	
G x N	2	0.0580	
Error	18		25.423

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Error mean square.
4 Level of pasture competition.
5 Monthly addition of N.

Appendix 10.3 **Summary of ANCOVA of ratio of increment in aboveground biomass:increment in aboveground nitrogen content of *P. radiata* using initial root collar diameter[2].**

	df[1]	P[2]	EMS[3]
G[4]	2	0.5847	
Pasture v. no pasture	1	0.4571	
Grazing v. rank	1	0.4786	
N[5]	1	0.1488	
G x N	2	0.8543	
Covariate	1	0.0001	
Error	17		106.2
Test of separate slopes		0.7367	

1 Degrees of freedom.
2 Probability of treatment differences according to ANCOVA or, where appropriate, probability of differences between specified contrasts.
3 Error mean square.
4 Level of pasture competition.
5 Monthly addition of N.